JOURNAL OF AGRICULTURAL RESEARCH

VOL. 60 WASHINGTON, D. C., JUNE 15, 1940 No. 12

STUDIES ON THE NATURAL INOCULATION OF SEED BARLEY WITH COVERED SMUT (USTILAGO HORDEI) [1]

By V. F. TAPKE

Pathologist, Division of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture

INTRODUCTION

The present investigation is one in a series of studies by the writer (*38, 39, 40, 42, 43, 44, 45*)[2] on inoculation, incubation, and infection in the smuts of barley (*Hordeum vulgare* L.) and was undertaken with a twofold objective: (1) To obtain a better fundamental knowledge of the natural method of inoculation and the reasons for its effectiveness and (2) to determine the cause of the usual ineffectiveness of the artificial method of seed inoculation and its exceptional effectiveness as reported by Faris (*11*).

PREVIOUS INVESTIGATIONS

Since Jensen (*23*) first reported, in 1888, two kinds of barley smut—loose smut (*Ustilago nuda* (Jens.) Kell. and Sw.) and covered smut (*U. hordei* (Pers.) Kell. and Sw.)—it has been singularly difficult to acquire an accurate knowledge as to how these smuts initiate, develop, and complete their parasitic relation with the barley host. For example, after it had been thoroughly established, apparently, that the barley loose smut fungus produces infection only through inoculation of the flowers (*4, 5, 7, 13, 17, 18, 21, 33*), up to 100 percent of loose smut was obtained through inoculating the seed (*48, 49*). Furthermore, seed treatment with certain surface disinfectants frequently was found highly effective in control (*30, 31, 46, 50, 51*) after convincing tests apparently had proved that only a long and penetrating seed treatment could reach and control the deep-seated infection threads of this smut (*2, 13, 22, 24*). In 1932 the writer (*38*) first reported that barley loose smut in the United States is caused not only by *Ustilago nuda* but also by another widespread fungus for which the name *U. nigra* was proposed. It was found that *U. nigra* is amenable to control through seed treatment with certain surface disinfectants and is able to produce seedling infection and smutted plants when the spores are superficially applied to the seed (*38, 39*). This discovery clarified the loose smut situation.

The barley covered smut, however, still remained difficult to understand. For example, it has been generally accepted that the firm, compact covered smut heads remain intact while they are in the field and that the seed first becomes inoculated in threshing, through disintegration of the smut heads and the adherence of spores to the surface of the kernels (*8, 10, 16, 19, 20, 22, 27, 34, 35, 37*). If this were

[1] Received for publication April 15, 1940. Cooperative investigations of the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, and the New York (Cornell) Agricultural Experiment Station.

[2] Italic numbers in parentheses refer to Literature Cited, p. 808.

entirely true, then the treatment of seed with a surface disinfectant should kill the superficially borne spores and control the smut. A wealth of literature is available, however, which shows that numerous liquid and dust fungicides applied to seed from smutted fields frequently have failed to effect complete control (*14, 28, 29, 31, 50, 51*). Moreover, if spores on the surface of seed were accountable for the heavy outbreaks of covered smut so frequently observed in growers' fields, then the artificial dusting of seed with millions of spores should prove an effective method of inoculation. Extensive tests over many years, in this country and in other countries, have shown repeatedly that this method of inoculation usually results only in low percentages of covered smut (*1, 3, 6, 23, 25, 32, 36, 47*). The effect of this predicament on the progress of research has been well epitomized by Mackie (*32*):

> Experiments in California have for three years failed in attempt to create heavy smut attacks by artificially inoculating seed barley. This has been the experience of other investigators. It has therefore been impossible to determine the smut resistance of any of the hundreds of barley varieties under test.

Adding further to the complexity of the situation, Faris (*11*), in diametric contrast to the usual experience, reported excellent results with the spore-dusting method of seed inoculation. There is nothing to indicate that the technique of inoculation used by Faris differed from that used by Mackie and others reporting unsatisfactory results with this method.

Pending the solution of the problem of inoculation noted above, covered smut has long continued an important hazard in barley culture in the United States. Annual losses estimated at 3 million to more than 5½ million bushels are not infrequent. In individual fields, 30 to 50 percent of covered smut has been reported.[3] It is therefore evident that the natural method of seed inoculation, whatever it may be, is highly effective.

EXPERIMENTAL RESULTS

LOCATION OF INOCULUM ON NATURALLY INOCULATED SEED

Procedure in the present investigation was influenced by the outstanding reports of Zade (*52, 53*) and Gage (*15*) on the seedling-infecting smuts of oats. As with the covered smut of barley, it had long been considered that spores of the oat smuts remained dormant after reaching the seed and that germination of the spores did not take place until the seed was sown and began to germinate. Zade discovered, however, that in the floral-inoculating loose smut of oats, the spores normally begin to germinate soon after reaching the flowers and that mycelium from the spores constitutes an effective subhull inoculum that is accountable for most of the infection of seedlings and subsequent smutting of heads. Later Gage found that, with both loose and covered smuts of oats, spores that reach the seed may

[3] UNITED STATES BUREAU OF PLANT INDUSTRY. ESTIMATE OF CROP LOSSES DUE TO PLANT DISEASES. 1917. U. S. Bur. Plant Indus., Plant Dis. Bul. 2: 1–18. 1918. [Mimeographed.]
——— CROP LOSSES FROM PLANT DISEASES IN THE UNITED STATES. 1918–38. U. S. Bur. Plant Indus. Plant Dis. Rptr. Sup. 6: 186–213, 1919. 12: 307–332, 1920. 18: 317–338, 1921. 24: 489–510, 1922. 30: 462–490 1923. 36: 318–348, 1924. 43: 381–410, 1925. 49: 382–412, 1926. 56: 394–423, 1927. 64: 370–399, 1928. 83: 1–68 1932. 87: 1–82, 1935. 89: 1–45, 1935. 94: 1–75, 1936. 100: 48–79, 1937. 108: 96–131, 1938. [Mimeographed.

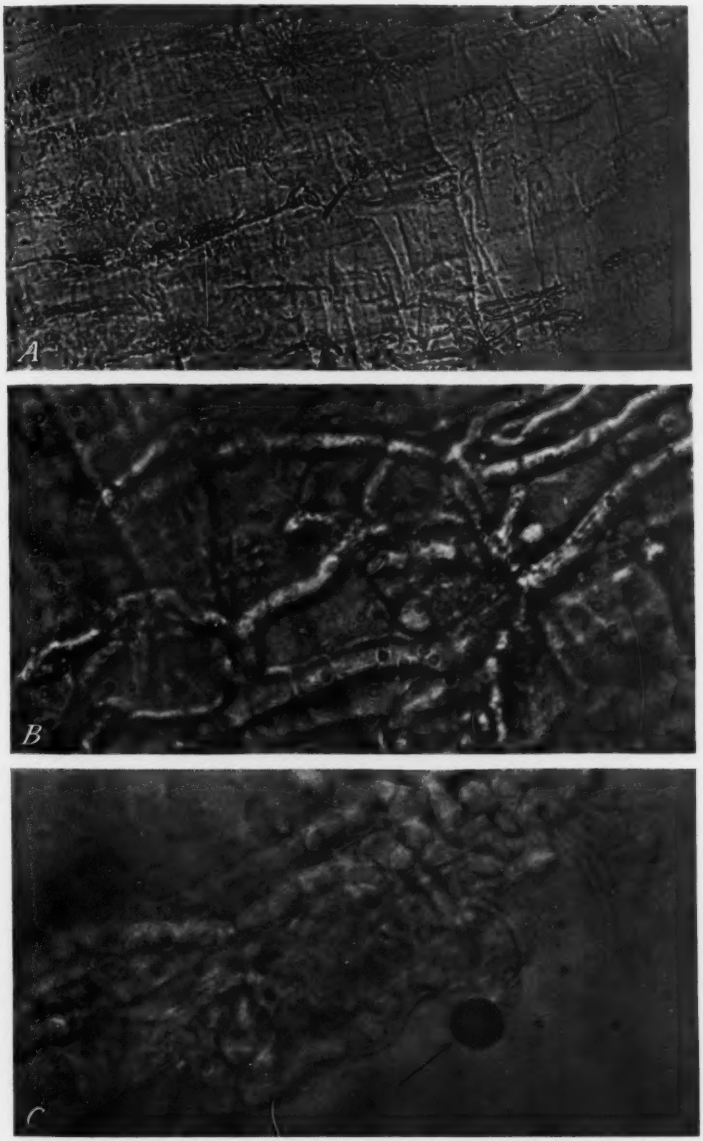
germinate not only during the blossoming period but also during the maturing period and even when the seed is in storage. Although differing with Zade in some details, Gage also found that inoculum beneath the hulls was largely responsible for most of the infection of seedlings and the subsequent smutting of heads. It seemed likely, therefore, that likewise in barley the most effective inoculum of covered smut, under natural conditions of inoculation, might be that which became lodged under the hulls of the seed. To determine whether this might occur, six hulled varieties of barley naturally inoculated with covered smut were studied. These barleys had been collected in Kansas, Maryland, Pennsylvania, Washington, and Wisconsin, from fields heavily infested with covered smut; all the fields, except that in Wisconsin, were practically free of loose smut. After being threshed and then stored in the growers' bins until the following late February or March, the seed was sent to the writer. During the 2 weeks preceding sowing, the hulls were carefully removed from some of the seed of each variety with the aid of a scalpel.

The experiment was designed also to throw light on two related phases. (1) Since the copper carbonate seed treatment frequently has been shown to be ineffective in the control of barley covered smut and the reasons for this have not been clearly understood, both normal and dehulled seed of the various lots were dusted with copper carbonate to determine the possible role of the hulls in protecting inoculum that might be carried beneath them. (2) In some previous studies with oats, dehulling the seed has been employed to determine not only the seed parts that harbor inoculum but also the approximate proportions of effective inoculum borne by the caryopsis and by the hulls. The writer (*41*) previously has shown that at least with oats this method is not reliable. The percentages of smutted plants from normal and dehulled seed maintain no consistent relation under different environmental conditions of seeding and plant growth. In order to determine whether this also might hold true with barley for covered smut, normal and dehulled seed, untreated or treated with copper carbonate, was sown at different times in the field and greenhouse at the Arlington Experiment Farm, Arlington, Va., and in the field at Ithaca, N. Y. (Cornell University). The results are presented in table 1.

It will be noted in table 1 that: (1) Plants from the dehulled seed showed, on an average, approximately three-fourths as much smut (24.9 percent) as the plants from seed with the hulls on (33.5 percent). This is evidence of the occurrence of subhull inoculum in seed lots from eastern, western, and central areas of the country and of the high degree of effectiveness of this inoculum under various field and greenhouse conditions; (2) the copper carbonate seed treatment completely controlled covered smut when applied to dehulled seed but not when applied to seed with hulls on. The frequently noted ineffectiveness of the copper carbonate seed treatment against barley covered smut thus would seem to be due to the fact that, in nature, inoculum may occur beneath the hulls and the hulls may protect this inoculum to some extent from the lethal action of the disinfectant.

TABLE 1.—*Incidence of covered smut in barley as influenced by removing the hulls from naturally inoculated seed and sowing the dehulled and normal seed under various conditions, and the effectiveness of the copper carbonate seed treatment in control of covered smut when applied to normal and dehulled seed*

Seed lot No.	Variety and source	Location of experiment	Date of seeding	Heads of barley grown from seed in indicated condition								
				Seed untreated					Seed treated			
				Hulls on		Hulls removed		Increase (+) or decrease (−) in smutted heads resulting from removal of hulls	Hulls on		Hulls removed	
				Total heads	Smutted heads	Total heads	Smutted heads		Total heads	Smutted heads	Total heads	Smutted heads
				Number	*Percent*	*Number*	*Percent*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1	Stavropol (Kansas, 1934)	Greenhouse, Arlington, Va	March 1935	108	58.3	114	34.2	−41.3	120	5.0	138	0
		Field, Ithaca, N. Y	April 1935	180	6.7	166	7.2	+7.5			133	0
2	Colsess (Washington, 1934).	Greenhouse, Arlington, Va	March 1935	120	87.5	135	73.3	−16.2	132	9.1	183	0
		Field, Ithaca, N. Y	April 1935	176	14.2	108	13.0	−8.5			116	0
		Greenhouse, Arlington, Va	March 1936	168	97.6	93	68.8	−29.5				
		Field, Arlington, Va	do	215	13.5	239	5.4	−60.0				
3	White Club (Washington, 1934).	Greenhouse, Arlington, Va	March 1935	114	52.6	87	75.9	+44.3	159	9.4	141	0
4	Alpha (Pennsylvania, 1934).	do	do	204	66.2	33	45.5	−31.3	201	7.5	21	0
		Field, Ithaca, N. Y	April 1935	248	4.4	143	7.0	+59.1			82	0
5	Tennessee Winter (Maryland, 1934).	Greenhouse, Arlington, Va	March 1935	104	38.5	60	56.7	+47.3				
6	Wisconsin Pedigree No. 5 (Wisconsin, 1928).	do	November 1929	231	19.5	198	19.7	+1.0				
		do	March 1930	259	9.3	256	.8	−91.4				
Total or average				2,127	33.5	1,632	24.9	−25.7				



A, Portion of a pericarp of Colsess barley (seed lot 2, table 1) from a field heavily infested with covered smut (× 210). *B*, Portion of the same pericarp, showing the ramifying, septate mycelium (× 940). *C*, Another part of the same pericarp; the septate mycelium appears to have emanated from the covered smut spore indicated by arrow (× 940).

A further analysis of the data of table 1 shows that the reduction in smutted heads resulting from dehulling the seed varied widely in the different lots sown under similar conditions and also in the individual lots sown under the different conditions of field and greenhouse. In 5 of the 12 tests, dehulling resulted not in a reduction but in an increase of covered smut. It seems evident, therefore, that in barley, as in oats, removal of the hulls from naturally inoculated seed does more than merely eliminate the inoculum that may be carried by the hulls. Evidently the hulls also exert some influence in tempering the environmental conditions surrounding the caryopsis, and their removal may lead to conditions that promote a greater or a lessened effectiveness in infection from the portion of inoculum that remains with the caryopsis. The amount of reduction in smut plants or heads resulting from removal of the hulls, therefore, cannot be used reliably to indicate the proportion of the inoculum carried by the hulls.

MICROSCOPIC STUDIES OF INOCULUM RESIDING WITH THE PERICARPS OF NATURALLY INOCULATED SEED

In a microscopic study of seeds from the various lots noted in table 1, covered smut spores and an abundance of septate mycelium of a definite type commonly were found with the pericarps of the caryopses (pl. 1, *A* and *B*). In several instances the characteristic mycelium was found emanating from covered smut spores (pl. 1, *C*). Presumably, therefore, the commonly observed mycelium was that of *Ustilago hordei*. The high percentages of smutted plants so frequently obtained from dehulled seed (table 1) also indicate that the heavy load of pericarp inoculum was that of *U. hordei*.

CONCLUSIONS BASED ON STUDIES OF NATURALLY INOCULATED SEED

The foregoing results failed to substantiate the long-held belief that spores on the surface of seed constitute the prime source of infection. It would appear, instead, that inoculum, in the form of spores and mycelium from germinated spores, on and in the pericarp of the caryopsis, accounts for most of the covered smut in plants from seed lots grown, handled, and stored under farm conditions. This apparently explains one of the perplexing angles of the problem previously noted (p. 788), i. e., the frequent heavy outbreaks of covered smut in crops from naturally inoculated seed on which inoculum is not macroscopically visible and the infrequent occurrence of smut in crops from seed artificially blackened with millions of spores. Inoculum lying beneath the hulls, close to the embryo and having unobstructed access to it, manifestly might be expected to be far more effective than inoculum on the outside of the hulls. In fact, it has recently been discovered that the position of inoculum on the seed is related not only to the speed and degree of seedling infection before emergence, but also to the influence of environment after emergence on the severity of both covered smut in barley and loose smut in oats (*44*, *45*). The foregoing results probably also explain the effectiveness of the spore-suspension method of inoculating seed barley with covered smut (*40*). According to this method, spores are washed beneath the hulls and the inoculated seed then is stored in a moistened condition for

24 hours to permit the spores to germinate. The method thus simulates the effective natural method of initiating infection through inoculation of the caryopsis. It is noteworthy that Jensen (*23*), Tisdale (*47*), Faris (*12*), Briggs (*6*), Johnston (*25*), and Aamodt and Johnston (*1*) likewise have reported good infection through inoculation of the caryopsis by dusting with spores after the hulls had been removed. The practical difficulties in removing the hulls, however, have prevented a wider use of this effective method.

DIFFERENT TYPES OF EMERGENCE OF COVERED SMUT HEADS AND THEIR RELATION TO SPORE DISSEMINATION AND SEED INOCULATION

In view of the foregoing results, observations were made on the type of emergence of smutted heads, and experiments were undertaken to determine, under field conditions at Arlington farm, how soon after heading the dissemination of spores and inoculation of seed begins, how long it continues, and its relative importance in different periods of seed development and in threshing. Also, the influence of different conditions during storage on the germination of seed-borne spores and on the effectiveness of different seed treatments throughout the various phases of the host-pathogen association were studied.

In regard to spore dissemination and seed inoculation in nature, a factor should be noted that may have a material influence on these processes. Apparently it has not been previously reported that there are different types of covered smut heads in respect to emergence. For example, when Odessa (C. I.[4] 934) spring barley was grown in a greenhouse from seed inoculated with the writer's physiologic race 4 (*43*), the smutted heads failed to reach the auricles of the flag leaf. They emerged laterally and usually remained partly sheathed as shown in figure 1, A. However, when Odessa was similarly grown from seed inoculated with physiologic race 1, the smutted heads emerged completely above the boot (fig. 1, *C*). In addition to the race of smut, the variety of barley and the growing conditions apparently also may be concerned. All of the plants shown in figure 2, for example, were grown from seed similarly inoculated with spores from a single purified collection (collection 13, race 6). The winter barleys Alaska (C. I. 4106) and Nobarb (C. I. 6120) produced exserted smut heads, but the spring variety White Smyrna (C. I. 910) produced the low, semienclosed type. These three barleys were grown in adjacent rows under winter conditions at Arlington farm. When the Alaska plants were grown under greenhouse conditions, however, they produced semienclosed smut heads.

In the following studies on dissemination of inoculum and inoculation of seed, the exserted type of covered smut head was principally concerned. Based on observations to date, this seems to be the prevailing type in the standard winter barleys grown in the field at Arlington farm. It would seem likely that the greater exposure of exserted heads to wind and rain and to contact with the awns and barbs of normal heads would result in an earlier and more complete dissemination of spores before threshing than would the protected position of

[4] C. I. refers to accession number of Division of Cereal Crops and Diseases, formerly Office of Cereal Investigations.

smutted heads that are more or less enclosed. Therefore the local prevailing type of both smutted heads and weather conditions may be concerned in various degrees in the time and manner of spore dis-

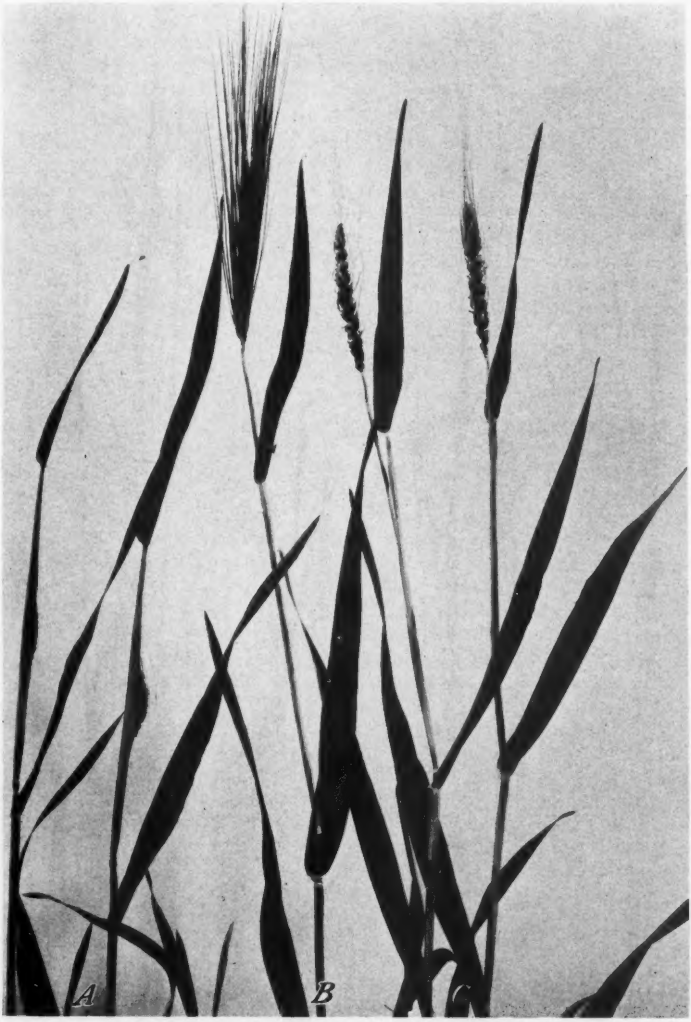
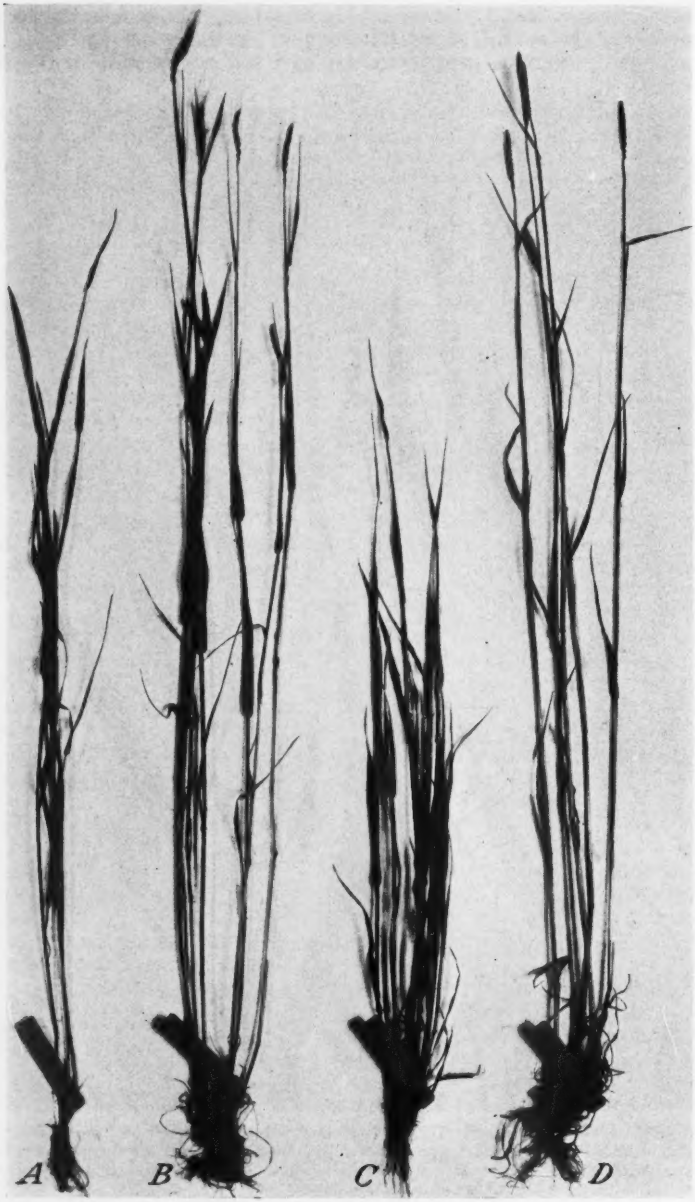


FIGURE 1.—Influence of different physiologic races of covered smut on type of smut heads in Odessa barley. *A*, Low, semienclosed smut heads; seed inoculated with spores of race 4. *B*, Normal head. *C*, High, exserted smut heads; seed inoculated with spores of race 1.

semination and seed inoculation. This is a possibility that doubtless should be considered in applying the present results to the wide variety of conditions under which barley is grown.



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In the light of the foregoing data, it is of interest to note that, in the literature also, the descriptions of covered smut heads frequently indicate that different types were being described, at least with respect to persistence of the smut-enclosing membrane and dissemination of spores. Frequently it is stated that the spores of barley covered smut are mostly or entirely confined to the heads by membranes that persist until the crop is threshed (*8*, *10*, *19*, *20*, *22*, *27*, *34*, *35*, *37*). But Güssow and Conners (*16*) note that covered smut in the field "may be mistaken for loose smut, which it resembles at times rather closely." Likewise, according to Clinton (*9*), the general appearance of loose and covered smuts—

> is such as to lead one to suppose them to be the same, since they both occur as dusty outbreaks which more or less completely destroy the flower parts; [however, the covered smut] has these outbreaks protected by a membrane which thus more permanently holds the spores together.

Kellerman and Swingle (*26*) note that—

> the covered barley smut differs from all the other loose smuts in that the attacked panicle is not at once converted into a powdery mass by the escape of the smut, but the smut remains more or less completely enclosed by a membrane [that] keeps the smut intact for some time and finally allows it to escape through rents and fissures in the membrane.

DISSEMINATION OF COVERED SMUT IN WINTER BARLEYS AT ARLINGTON FARM

The writer's observations on covered smut in the standard varieties of winter barley grown in the field at the Arlington Experiment Farm confirm those of Kellerman and Swingle noted above. A few days after the smutted heads emerge, the membranes of the sori begin to develop rents and fissures. The spore masses thus exposed become dry and powdery, and spores may be readily blown, washed, or otherwise carried to healthy heads (fig. 3). Moreover, as the plants and normal heads become dry and brittle with maturity, the smutted heads likewise undergo a process of ripening and become dry and spongy. Further splitting of peridia and dispersal of spores accompanies this process (fig. 4). The disintegration of sori and the dissemination of spores also are promoted by the moving contact of smutted and healthy heads as they wave in the breezes during the period from heading to cutting. The barbs of rough-awn barleys are especially effective in shredding the spore-enclosing membranes. Disintegration of covered smut heads in a plot of ripened, standing Wisconsin Winter barley at Arlington farm in 1936 is shown in figure 5, *A*. It is evident that much of the covered smut was disseminated before this grain was cut. In cutting, binding, and shocking the grain, a further dissemination of spores doubtless occurred. Finally, conditions in the shock that accompany curing and drying, at least at Arlington farm, increase further the fragility of peridia and powderiness of the smut. A representative sample of covered smut heads

Explanatory legend for figure 2

FIGURE 2.—Influence of environment (*A* and *B*) and of different varieties (*B*, *C*, and *D*) on type of covered smut heads. *A*, Alaska winter barley grown in a greenhouse; smut heads low. *B*, Alaska grown in the field, smut heads high. *C*, White Smyrna spring barley grown in the field; smut heads low. *D*, Nobarb winter barley grown in the field; smut heads high. *A*, *B*, *C*, and *D* were grown from seed similarly inoculated with spores from a single purified collection of covered smut; *B*, *C*, and *D* were grown in adjacent rows under winter conditions.

taken from a shock of Wisconsin Winter barley at Arlington farm shortly before threshing in July 1935 is shown in figure 5, *B*. It is

FIGURE 3.—*A*, Healthy head; *B*, two covered smut heads; *C*, loose smut head of Wisconsin Winter barley, showing comparative extent of disintegration in covered smut and loose smut heads toward the close of the bloom period of healthy heads in May 1936 at Arlington farm. The enclosing membranes of the covered smut heads already had broken at that time.

apparent that under the conditions that prevailed, much of the smut-head disintegration, spore dissemination, and seed inoculation has preceded threshing.

In view of the fact that some of the covered smut heads resembled those infected with loose smut, it should be noted that especial care was taken to make sure that only covered smut was present. The crop from which these smutted heads were collected had been grown from seed treated with formaldehyde solution. After treatment, the seed was divided into 2 parts. One part was dusted with spores of *Ustilago hordei;* the other was not inoculated. Both parts were sown in the fall of 1934. The uninoculated seed produced a smut-free crop. The plants from inoculated seed produced 13 percent of covered smut heads. From this smutted crop, the 6 smut heads shown in figure 5,

FIGURE 4.—*A*, Covered smut heads of Han River barley, showing the progress of disintegration 2 weeks after emergence in May 1935, at Arlington farm; *B*, an enlargement of the lower portion of the left head in *A*, showing the rents and fissures in the smut-enclosing membranes, which permit the release and spread of countless numbers of spores to the developing seed of nearby healthy heads.

B, were collected. Spores from each head were microscopically examined and were germinated on 2-percent potato-dextrose agar. The spores were smooth-walled and on germination produced promycelia bearing typically 4 lateral sporidia, both characters typical of *U. hordei*. In November 1935, seed of Odessa barley that had been treated with a 1 : 320 formaldehyde solution for 2 hours at 20° C. was divided into 7 parts. One part was not inoculated; each of the others was inoculated with an aqueous suspension of spores from 1 of the smut heads. Sown in a greenhouse, the uninoculated seed produced a smut-free crop, while each of the inoculated lots produced 20 to 25

plants with 90 to 100 percent of smutted heads, all of which showed the external typical characters of covered smut. Furthermore, examination of the spores from each of the 6 lots showed that their walls were smooth, and on germinating they produced the typical pro-

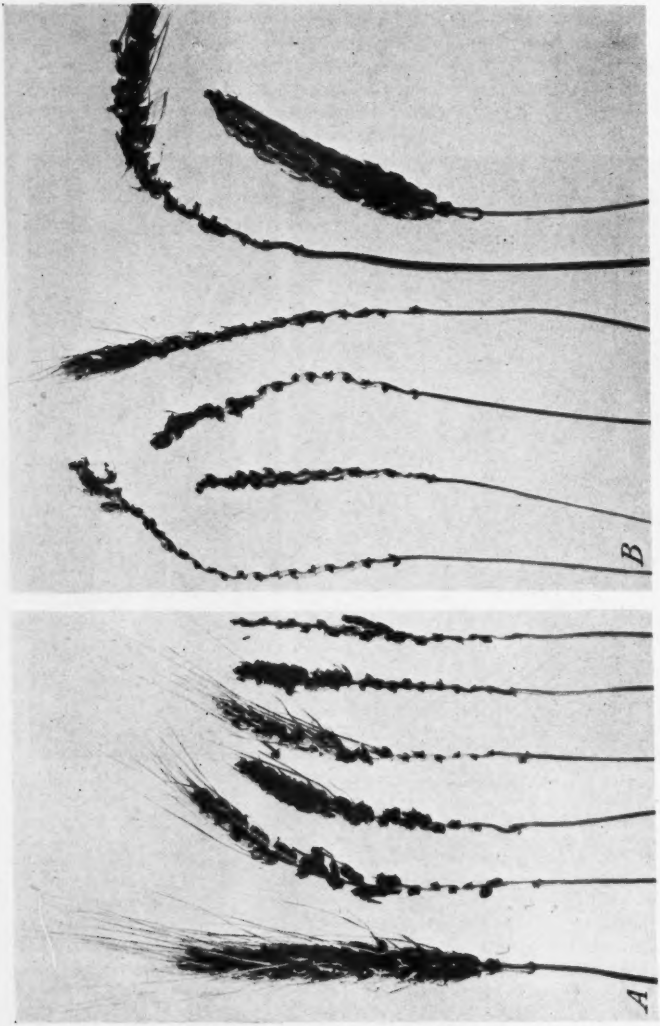

FIGURE 5.—Representative samples showing the progress of disintegration in covered smut heads of Wisconsin Winter barley at Arlington farm: *A*, Heads collected from standing plants a day before the grain was cut in June 1936; *B*, heads collected from a shock a few days before threshing in July 1935.

mycelium with lateral sporidia. There can be no doubt, therefore, that the heads shown in figure 5, *B*, were infected with true covered smut.

In view of these data, it seems evident that, at least under the weather conditions and with the exserted type of covered smut heads

at Arlington farm, a considerable portion of covered smut spores may be disseminated not only before the barley is threshed but even before the grain is cut.

EFFECTS OF PERIODS OF SPORE DISSEMINATION AND METHODS OF SEED STORAGE

In the light of the foregoing observations, a practical question arises as to how the severity of covered smut in the next crop is affected by spore dissemination in different periods of development of the seed barley and of different methods of seed storage.

Simultaneously with the studies on spore dissemination, experiments were conducted to determine the effectiveness of inoculum distributed to the seed (1) while still in the heads of standing plants; (2) as a result of the cutting, binding, and storage of grain in the shock; and (3) as a result of threshing. The influence of some conditions under which inoculated seed may be stored after threshing was also studied. Through this procedure it was possible to trace, step by step, the inception and early development of the host-parasite relation and to determine the importance of each step in the ultimate development of covered smut.

In a preliminary study, covered smut heads (fig. 4) were collected at Arlington farm in May 1935 from field-grown Han River winter barley. A few days later, spores sifted from the smutted heads were applied dry, by means of a small brush, to healthy heads of Cusado (C. I. 895) and Han River (C. I. 2163) barleys growing in an isolated smut-free plot. The heads thus inoculated had emerged about 2 weeks previously. At maturity in June, the inoculated heads were placed in a desiccator over calcium chloride in order to dry thoroughly and to inhibit any further development of the inoculum. After being stored in this manner until the following November, the heads were threshed by hand. After threshing, the seed was immediately returned to the desiccator except that a portion from each variety was soaked in a 1:320 formaldehyde solution at 20° C. for 1 hour, then washed in water and spread in a thin layer to dry. After 3 days this seed was sown in a greenhouse, together with the remaining seed from the desiccator. A part of the latter was treated with copper carbonate dust (50 percent copper) immediately before sowing, while another part was sown without treatment. The results are presented in table 2.

TABLE 2.—*Covered smut resulting from brushing dry spores on Cusado and Han River barley heads 2 weeks after their emergence at Arlington farm, and the smut-controlling effects of copper carbonate dust and formaldehyde solution when applied to seed from the inoculated heads*

Seed treatment	Heads of Cusado		Heads of Han River	
	Total	Smutted	Total	Smutted
	Number	*Percent*	*Number*	*Percent*
None	123	82.9	120	86.7
Copper carbonate dust	119	73.1	131	48.9
Formaldehyde solution	118	18.6	119	7.6

The data in table 2 show clearly that covered smut spores reaching immature barley seed in the heads of standing plants may result in

very high infection. Smut was only moderately reduced through treating the seed with copper carbonate and was not completely controlled, even after treating the seed for 1 hour with the formaldehyde solution. In view of these facts there can hardly be any doubt that some of the inoculum, probably in the form of mycelium from germinated spores, got beneath the hulls, where it was protected against the lethal action of the disinfectants.

In a further study of spore dissemination and seed inoculation, healthy heads of Wisconsin Winter barley were collected in July 1935 from a shock immediately before it was threshed. From the same shock, the smut heads shown in figure 5 *B*, also were collected. As noted previously (p. 796) only one smut was present in the crop and it was definitely identified as *Ustilago hordei*. Immediately after their collection, the healthy heads were placed in a desiccator over calcium chloride in order to dry the seed thoroughly and to inhibit any further development of inoculum that may have reached it. The following day a portion of the threshed seed also was placed in a desiccator immediately after threshing, and another portion, consisting of 2 bushels of threshed seed, was put in a grain sack and stored in a laboratory. After being stored in this manner until the following November, each lot was divided into three portions and, as in the previous test, one was treated with copper carbonate dust (50 percent copper) and one with formaldehyde solution, while the third was left untreated. These various lots were then sown in a greenhouse. The results are presented in table 3.

TABLE 3.—*Relative importance in 1935 of spores distributed to seed before and during threshing on the occurrence of covered smut in Wisconsin Winter barley, and influence of 2 methods of storing threshed inoculated seed and of treating seed (with copper carbonate dust or formaldehyde solution) on the loss from smut*

Source of seed	Method of storing seed, July to November	Method of treating seed, following storage	Heads	
			Total	Smutted
			Number	*Percent*
Shock	Stored in desiccator over calcium chloride in laboratory.	Untreated	75	70.7
		Copper carbonate	70	35.7
		Formaldehyde solution	79	2.5
Threshing machine	do	Untreated	70	81.4
		Copper carbonate	72	51.4
		Formaldehyde solution	70	1.4
Do	Stored in 2-bushel bag in laboratory.	Untreated	77	90.9
		Copper carbonate	73	39.7
		Formaldehyde solution	74	2.7

It will be noted in table 3 that (1) the naturally distributed inoculum on the seed before threshing resulted in a high percentage of covered smut; (2) the additional inoculum added to the seed in threshing effected a further increase of smut; and (3) the storage of threshed inoculated seed in bulk in a bag instead of storage in a desiccator resulted in an additional increase of smut. As in the preceding experiment, copper carbonate treatment of the seed proved ineffective in control, and even the 1-hour seed treatment with formaldehyde solution failed to give complete control.

In view of the definite indications of the preceding experiments on spore dissemination, the study was expanded in 1936–37 to include the complete range over which the pathogen is associated with the seed, i. e., from heading through seed development, harvest, threshing, and storage to the time of seeding. Seed of two varieties, Han River and Wisconsin Winter, was treated with formaldehyde solution, inoculated with *Ustilago hordei* by the spore-suspension method (*40*), and sown in 1/80-acre plots at Arlington farm in the fall of 1936. The following spring the Han River and Wisconsin Winter plots developed 26.2 and 33.4 percent of covered smut heads, respectively. Normal heads in these plots were collected at random from standing plants the day before each crop was cut. Later, heads were collected from shocks the day before the barley was threshed. In both cases the heads, immediately after collection, were placed in desiccators in the laboratory. Following threshing, a few hundred threshed seeds were immediately placed in a desiccator. Also 2 bushels of threshed seed was placed in a grain sack and stored in the laboratory near the seed in the desiccators. Seed of the various lots was stored as indicated from June to October 1936 and then divided in two portions, one of which was untreated and the other treated with copper carbonate dust (50 percent copper). Immediately thereafter, the seed was uniformly sown in special containers in which soil conditions highly favorable to infection were maintained. When the seedlings were 1 to 1½ inches above the soil they were transplanted to an outdoor plot. The results are presented in table 4.

The data in table 4 give a vivid picture of how the covered smut fungus progressively enhanced its relation with the host throughout the development, ripening, curing, threshing, and storage of the barley seed. The naturally distributed inoculum on the seed before cutting resulted in an average of 19.5 percent of smutted heads in the two varieties. The inoculum added to the seed as a result of cutting and shocking the grain raised the average to 27.1 percent. Inoculum added to the seed through final disintegration of the smutted heads in threshing brought the average to 50.6 percent. Finally, storage of the seed in bulk under prevailing atmospheric conditions evidently furnished the moisture that led to a further increase in the load of inoculum through germination of the seed-borne spores and spread of mycelium, with the result that an average of 71.3 percent of the heads were smutted. The marked increase in smut from storage of seed in a bag, as compared with that stored under very dry conditions in a desiccator, confirms the evidence of the previous year (table 3) that conditions of atmospheric humidity under which the seed is stored may have an appreciable influence on the development of inoculum borne by the seed and on the severity of smut infection. The ineffectiveness of the copper carbonate seed treatment throughout the test would seem to indicate that in these seed lots, as in the naturally inoculated lots from other parts of the country that were studied earlier (table 1), much of the effective inoculum in the form of spores or mycelium from germinated spores had passed beneath the hulls, where it was protected from the disinfectant.

TABLE 4.—*Relative importance in 1936 of different periods of spore dissemination; the influence of 2 different methods of storing threshed, inoculated seed; and the effectiveness of treating seed with copper carbonate dust on the loss from covered smut*

Variety and period of spore dissemination	Source of seed and date of collection in 1936	Method of storing seed from collecting to sowing (June to October 1936)	Seed treatment following storage	Heads	
				Total	Smutted
				Number	*Percent*
Han River:					
Day before cutting	Ripened heads of standing plants, June 9	Stored in desiccator	Untreated	183	21.9
Do	do	do	Copper carbonate	169	20.1
Day before threshing	Heads in a shock, June 29	do	Untreated	187	34.2
Do	do	do	Copper carbonate	179	21.8
Immediately after threshing	Threshing machine, June 30	do	Untreated	257	53.3
Do	do	do	Copper carbonate	236	48.3
Do	do	2 bushels stored in grain sack	Untreated	209	70.8
Do	do	do	Copper carbonate	199	70.4
Wisconsin Winter:					
Day before cutting	Ripened heads of standing plants, June 9	Stored in desiccator	Untreated	161	16.8
Do	do	do	Copper carbonate	159	4.4
Day before threshing	Heads in a shock, June 29	do	Untreated	152	18.4
Do	do	do	Copper carbonate	154	9.7
Immediately after threshing	Threshing machine, June 30	do	Untreated	209	47.4
Do	do	do	Copper carbonate	213	39.0
Do	do	2 bushels stored in grain sack	Untreated	191	71.7
Do	do	do	Copper carbonate	230	53.9
Both varieties:					
Day before cutting	Ripened heads of standing plants, June 9	Stored in desiccator	Untreated	344	19.5
Do	do	do	Copper carbonate	328	12.5
Day before threshing	Heads in a shock, June 29	do	Untreated	339	27.1
Do	do	do	Copper carbonate	333	16.2
Immediately after threshing	Threshing machine, June 30	do	Untreated	466	50.6
Do	do	do	Copper carbonate	449	43.9
Do	do	2 bushels stored in grain sack	Untreated	400	71.3
Do	do	do	Copper carbonate	429	61.5

In view of the fact that seed barley in the United States is harvested and stored under a wide range of moisture conditions, the influence of different atmospheric humidities during seed storage on severity and control of covered smut was studied further. The lot of barley used was a hulled variety (Norway, C. I. 2535), definitely known to harbor no naturally deposited smut inoculum. The seed was artificially blackened with spores and each of 6 lots (200 seeds per lot) was placed in a small wire basket suspended midway within a 1-pint mason jar. No water was added to the first jar, and 5, 10, 15, 20, and 25 drops of water were placed in the second to sixth jars, respectively. The water was deposited within each jar by means of a pipette so that none of the fluid touched the suspended seed. Immediately thereafter each jar was tightly sealed and stored in a 20° C. chamber for 1 month. The seed was then removed from the jars, and each of the 6 lots was divided into 2 equal parts, 1 of which was left untreated, the other treated with copper carbonate dust (50 percent copper). The seed then was sown in a greenhouse The results (table 5) show clearly that different degrees of atmospheric moisture to which inoculated seed is exposed in storage may markedly influence the incidence of covered smut in the succeeding crop and also the effectiveness of a seed disinfectant. Gage (*15*) has reported similar results with oat smut. The fact that copper carbonate failed to control the smut on seed stored under more humid conditions would seem to indicate that under those conditions the spores germinated in storage and developed a mycelium that grew beneath the hulls, where it was protected from the disinfectant. In the bottles with 20 and 25 drops of water, the increasingly heavy growth of mold that developed on the seed in storage probably interfered with development of the smut and doubtless accounts for the lower percentages of infection.

TABLE 5.—*Incidence of covered smut in Norway barley as influenced by storing seed superficially blackened with spores under different atmospheric humidities for 1 month at 20° C., and the influence of the different humidities during storage on the effectiveness of the copper carbonate seed treatment applied immediately after storage*

Drops of water in storage jar	Plants from seed given indicated treatment after storage				Mold on seed at conclusion of storage period
	None		Copper carbonate		
	Total plants	Smutted plants	Total plants	Smutted plants	
	Number	*Percent*	*Number*	*Percent*	
0	92	60.9	100	0	No visible mold.
5	84	69.0	84	0	Do.
10	72	75.0	96	0	Do.
15	80	87.5	100	28.0	Slight growth of mold.
20	92	82.6	98	18.4	Moderate growth of mold.
25	76	36.8	92	8.7	Heavy growth of mold.

In connection with these results it may be noted that seed treatment with copper carbonate dust has not been effective enough to warrant general recommendation. However, in California, according to Mackie (*32*), thorough and repeated dusting of the seed with copper carbonate every year appears to eliminate covered smut satisfactorily.

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Under dry conditions of harvest and storage in California, or elsewhere, spores that reach the seed possibly may not germinate and the inoculum therefore may remain largely confined to the seed surface, where it would be susceptible to control with copper carbonate.

In view of the foregoing findings on spore dissemination and seed inoculation, it is evident that, from the time the smutted heads emerge to the time the seed is sown, environmental factors and the conditions of handling and storing the smutted seed play an important role in the incidence of covered smut in the succeeding crop. Through their influence on the dissemination of spores and on the germination of spores after reaching the seed, environmental factors and handling and storage conditions are importantly related to the load of inoculum carried by the seed, the position of the inoculum in relation to the embryo, and the effectiveness of seed treatments for control. When it is further considered that the incidence of covered smut in barley may be markedly influenced by the interaction of various soil conditions from seeding to emergence (*11*), by environmental conditions after the seedlings have emerged (*44*, *45*), and by the various degrees of varietal susceptibility to the various physiologic races of the covered smut fungus (*12*, *43*), the multiplicity of interacting environmental and biologic factors concerned in the ultimate incidence of this smut in barley becomes apparent.

DISCUSSION

As already noted (p. 787), the inoculation of seed barley with covered smut has been difficult to understand. Naturally inoculated seed frequently has produced heavily smutted crops, while seed artificially blackened with millions of spores usually has produced crops with a surprisingly low incidence of smut. The factors underlying Faris' (*11*) exceptional success with the spore-dusting method likewise have not been understood. With the facts brought to light in the present study and with the aid of other data recently found on the nature of infection (*44*, *45*), it seems possible now to explain these discrepancies.

The present study has clearly shown that, in the successful natural method of seed inoculation, much of the effective inoculum becomes established beneath the hulls. In the ineffective artificial method, however, the inoculum is deposited on the exterior of the hulls. It would seem reasonable that inoculum residing on the caryopsis and having immediate and unobstructed access to the embryo should be able to invade the seedling more rapidly and effectively during its subterranean growth than inoculum elsewhere on the hulls. The different results from the natural and artificial methods of inoculation thus might be ascribed to the position of the inoculum on the seed relative to the hulls. As already noted (p. 788), however, certain results reported by Faris (*11*) definitely appear to challenge this hypothesis. By applying spores to the surface of Hannchen seed barley with the hulls intact, Faris obtained up to 97.8 percent of smutted plants. This would appear to be substantial evidence that the hulls were not effective barriers to infection. However, in the light of a recent discovery, it now appears that the hulls probably always interfere with infection but that their deterrent influence may be masked by a compensating factor. It has been found, recently, that the incidence of covered smut in barley and of loose smut in oats may be markedly

influenced by certain environmental conditions after the seedlings emerge (*44*, *45*). For example, the writer (*40*), inoculated seed by the superficial dusting method and also by the spore-suspension method, in which the inoculum is deposited beneath the seed hulls as with naturally inoculated seed. After the seed had germinated under controlled soil conditions favorable to infection, seedlings were transplanted in autumn or winter to a field or greenhouse. Field and greenhouse plants from seed inoculated by the spore-suspension method produced similar high percentages of smut.

When seed was inoculated by the superficial dusting method, plants grown in a greenhouse from emergence to maturity also produced a high percentage of smut but plants grown in the field after emergence produced only a low or appreciably lower percentage of smut. The superficial dusting method of inoculation therefore appeared effective when the plants were grown in a temperate environment after seedling emergence, and less effective or ineffective when the plants were grown after emergence under the colder, more rugged conditions to which winter grains are exposed in the field at Arlington farm. In the experiment of Faris with Hannchen spring barley noted above, success with the superficial dusting method of inoculation likewise was linked with a temperate post-emergence environment. In contrast, the investigators reporting unsatisfactory results with the dusting method of seed inoculation grew their plants under field conditions (*1*, *3*, *6*, *23*, *25*, *32*, *36*, *47*). It is noteworthy also that, in an experiment with two winter barleys, Faris (*12*) obtained no smut whatsoever when spore-dusted seed was germinated under soil conditions favorable to infection and the plants were grown in the field from seedling emergence in October to maturity the following summer. However, when the plants were grown in a greenhouse at 55° to 70° F. after emergence, considerable smut developed.

These results therefore seem to warrant the following conclusions in explanation of the difficulties in understanding the inoculation and infection of barley by the covered smut: In general, and within limits, the incidence of covered smut in plants from naturally inoculated seed frequently is high because inoculum finds its way beneath the hulls under natural conditions of inoculation. Through the advantage of proximity to the embryo, the pathogen is facilitated in establishing a deep-seated infection from seeding to seedling emergence. For infection of the seedling, therefore, the fungus becomes less dependent upon the uncertainty of favorable climatic conditions after emergence. When inoculum resides on the surface of seed, as happens when seed is artificially dusted with spores, it is evidently more difficult for the pathogen quickly to establish a deep-seated preemergence infection, owing to the obstructing hulls. Success with this method, then, depends more upon the hazard of a period of temperate climatic conditions after the seedlings emerge. In this account, it is assumed, of course, that the soil conditions from seeding to seedling emergence have been at least somewhat favorable for infection.

From the results of previous studies (*11*, *44*, *45*) and those of the present investigation, the host-parasite relation of barley and the covered smut fungus now may be traced from its inception at heading, through the ripening, harvesting, threshing, and storage of the seed, and from seeding through seedling emergence to maturity (*11*, *44*, *45*).

This information should serve a practical purpose in breeding for resistance to covered smut. It has already served a useful purpose in the development of the spore-suspension method of seed inoculation (*40*), a new artificial method patterned after the natural method, which is practicable and has been highly and consistently effective under field and greenhouse conditions of barley culture.

SUMMARY AND CONCLUSIONS

A practicable and effective artificial method of inoculating seed barley with covered smut has been diligently sought for many years. No satisfactory method being available, it has been difficult to determine adequately the smut resistance of barley varieties and to breed for resistance against the heavy annual toll of covered smut. Years of general observation have convincingly established the fact that inoculation of seed as it occurs in the usual field culture of barley is effective and frequently results in high percentages of smut. The object of the present study, therefore, was to determine the factor or factors responsible for the effectiveness of the natural method and to use the knowledge in developing a successful artificial method.

It has long been generally considered that, under the natural or field conditions of inoculation, spores of barley covered smut are held in the smutted heads until threshing and that inoculation comes about when the smutted heads are disintegrated in threshing and free spores stick to the surface of the seed hulls of barley. The artificial blackening of seed with millions of spores, however, repeatedly has failed to result in good infections. Furthermore, the treatment of naturally inoculated seed with certain surface disinfectants usually has failed to result in satisfactory control, indicating that the effective inoculum is beneath rather than upon the seed hulls.

Through a study of naturally inoculated seed lots from Eastern, Central, and Western States it was found that the most effective inoculum consisted not of spores upon the seed hulls but of spores and of extensive ramifications of mycelium from germinated spores on the pericarps of the caryopses beneath the seed hulls. The occurrence of this subhull inoculum in nature evidently explains why copper carbonate dust, formaldehyde solution, and some other surface disinfectants of seed barley repeatedly have been reported as being relatively ineffective in the control of covered smut throughout most of the barley-growing areas of the United States.

In the light of another discovery on the covered smut of barley that has been recently reported, it seems possible now to explain also why the subhull inoculum of naturally inoculated seed has been generally effective and the superficial inoculum of artificially inoculated seed generally ineffective. It has been shown that when seed is sown and the inoculum is beneath the hulls, the pathogen is frequently able to establish such a deep-seated infection of the seedling before it emerges that exposure to cold after emergence has relatively little adverse influence on infection. When the inoculum resides on the exterior of the seed, however, the nature of the infection is such that exposure to cold after the seedlings emerge usually promotes a lowered incidence of smut. High infections may occur, but they are dependent on the hazard of a moderate climatic period of several weeks or more following emergence.

In a study of spore dissemination and seed inoculation in the field at Arlington Experiment Farm, Arlington, Va., it was found that all of the spores of barley covered smut are not held intact in the smutted heads until threshing, as has been generally reported. A few days after the smutted heads emerge, the membranes that enclose the spores begin to split, thus permitting an early dissemination of spores and an early inoculation of developing seed in healthy heads. Disintegration of smutted heads, dissemination of spores, and inoculation of seed continue throughout the development, maturation, curing, and drying of the standing and shocked grain, and culminate with the completion of threshing.

All of the spores that reach the seed do not lie dormant on the surface of hulls until seeding. Some that are blown, washed, or otherwise carried to the seed from heading to threshing time may come to lie beneath the hulls or send infection hyphae beneath the hulls or both. Likewise, spores that reach the seed during threshing also may send infection hyphae beneath the hulls under certain conditions of moisture during storage. Thus, beginning a few days after the smutted heads emerge and continuing to the time when the seed is sown, the pathogen may pursue its course in the subhull region of the seed.

The relative importance of dissemination of inoculum and seed inoculation during different periods of seed development and under different conditions of seed storage at Arlington farm was ascertained in 1935 and 1936. The results of both years were definite and similar in their indications that, from heading through ripening, cutting, shocking, threshing, and storage, the covered smut fungus progressively improved both its entrenchment in the subhull region of the seed and its relation to infection of the seedling upon seed germination.

In a further study of storage conditions, progressive increases in the atmospheric humidities in which inoculated seed was stored resulted in progressive increases in the incidence of covered smut, up to the point when the growth of mold on the seed became appreciable. Also, the copper carbonate dust treatment ceased to be effective in control when applied to seed stored at the higher humidities. The seed was artificially inoculated through blackening the surface with spores.

Two different types of emergence of covered smut heads are described and illustrated. In the one type, the smutted heads fail to reach the auricles of the flag leaf and remain half enclosed in the boot. In the other type, the smutted heads become fully exserted. The latter type chiefly occurs in the standard winter barleys at Arlington farm, and it was this type of covered smut that was used in the present study. Whether spores are disseminated more rapidly from the exserted than from the semienclosed type of covered smut head has not been determined. Intermediate and irregular types also have been observed. Preliminary studies seem to indicate that the variety of barley, the physiologic race of smut, and the conditions under which the plants are grown are factors concerned in the different types of emergence of the smutted head.

The recently extended knowledge of factors that condition the infection of barley by *Ustilago hordei* has aided in the development of the spore-suspension method of seed inoculation. This is a new artificial method, patterned after the natural method, that has proved to be highly and consistently effective as well as practicable.

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FOLIAR DIAGNOSIS OF DIFFERENTIALLY FERTILIZED GREENHOUSE TOMATOES WITH AND WITHOUT MANURE[1]

By WALTER THOMAS, *professor of plant nutrition*, and WARREN B. MACK, *professor of vegetable gardening, Pennsylvania Agricultural Experiment Station*

INTRODUCTION

The method of foliar diagnosis (*4*)[2] has demonstrated that deductions drawn solely from observations of the relations between the fertilizer applied and the yields are very restricted and may not infrequently be erroneous (*5*, *6*).

Such errors result from lack of knowledge of the processes of nutrition which have determined the yields. To illustrate: A fertilizer element may be absorbed and utilized by the plant and yet its application may result in a reduction in yields through its effect on the absorption of another element (*7*, *8*). In the present experiment, the yields alone would have given no indication that the higher yields of the manured over the unmanured plots taken as a group were due to the higher level of potash nutrition produced by the manure.

The method of foliar diagnosis has not, thus far, been applied to plants of the indeterminate type of growth, such as tomatoes under glass. Certain statements, frequently met with in the literature, to the effect that artificial conditions in a greenhouse result in obscuring or obliterating the specific effects of mineral nutrients on leaf development would possibly lead to the conclusion that the method of foliar diagnosis fails to show any relationship between the mineral nutrition and the development of the plant. But, as the results reported herein show, such a conclusion would be erroneous. The fallacy lies in the failure to recognize the fundamental principle inherent in the method of foliar diagnosis, namely, that in the examination of the nutrition of morphologically homologous leaves sampled from plants at the same time, the values are used in a comparative manner only (*2*).

MATERIAL AND METHODS

DESCRIPTION OF THE BEDS

A detailed description of the beds and also of the method of culture of the plants has been given by Mack (*1*). Each bed is divided into 2 plots of equal size, 5¾ feet wide by 8 feet long, with 12 plants in 3 rows of 4 plants each, lengthwise of the plot. The surface soil is a composted clay loam, 14 inches in depth, with a clay loam subsoil. The plants in the experiment reported in this paper were selected for uniformity and were grown from seed of a Pennsylvania certified strain of the Marglobe variety of tomatoes (*Lycopersicum esculentum* Mill.).

Each pair of plots in a bed received the same fertilizer treatment, but one of them received in addition an annual application of well-rotted horse manure just before the fall crop was planted.

[1] Received for publication October 30, 1939. Paper No. 929 in the Journal Series of the Pennsylvania Agricultural Experiment Station.

[2] Italic numbers in parentheses refer to Literature Cited, p. 832.

THE FERTILIZER APPLIED

The fertilizer treatments consisted of a single element, combinations of two elements, and also of all three elements at the rate of 260.8 gm. of sodium nitrate, 625.9 gm. of superphosphate, and 95.2 gm. of muriate of potash per plot, equivalent to 41.73 gm. of N, 125.19 gm. of P_2O_5, and 43.1 gm. of K_2O. The single applications were equivalent to 500 pounds of nitrate of soda, 1,250 pounds of superphosphate, and 350 pounds of muriate of potash to the acre. Manure was applied at the rate of 110 pounds per plot, equivalent to 50 tons to the acre. This quantity (110 pounds) contained 424.1 gm. of N, 279.4 gm. of P_2O_5, and 344.3 gm. of K_2O. No in vitro tests of indisputable validity are known for determining the availability of the fertilizer elements in manure. In the present experiment the availability of the elements could be gauged from the results on the plot which received manure only.

The different treatments are shown in table 1 in which N, P, and K designate the amounts of the respective carriers, (2N) twice the amount, and (RN) biweekly applications of the standard amount of nitrogen throughout the growing period; this was approximately equal to 2,086.4 gm. of nitrogen. The letter m indicates manure. The plants were watered when necessary by allowing water to run from a hose for the same length of time on each plot. Plants were set in the beds on March 9. They were trained to upright single stems, and the stem was cut off at a height of about 7 feet. Fruits were harvested when well-colored.

LEAF SAMPLING

Effective sampling from such a relatively small number of plants, 12 in each plot, presented difficulties, especially when individual differences among plants of a plot were quite marked in certain plots. In sampling plants grown under field conditions (*4*, *5*, *6*, *7*, *8*, *9*), leaf samples were not taken from those plants that deviated considerably from the average of the plot. This practice, if adopted in the greenhouse, would have given too small a sample; nor could the customary method of sampling plants lengthwise across a plot be adopted, for by carrying out such a system only 4 plants would have been available in each plot. The compromise adopted was to sample the fifth leaf from the base on all plants on a plot at 3 sampling dates, April 5, April 29, and May 17, as follows:

At the first sampling two or three leaflets were taken on one side of the midrib of the leaf; at the second sampling, the leaflets opposite those removed at the first were selected; and at the third sampling, the remaining lateral leaflets and the terminal leaflet were taken as a sample.

Owing to senescence of the fifth leaf on many of the poorly nourished plants, a fourth sampling was not possible 3 weeks after the third samples were taken. In plants of indeterminate type of growth, as in this experiment, it would have been possible to have extended the observations by using the method of relay sampling described in an earlier paper (*4*).

ANALYTICAL METHODS

The preparation of samples and the analytical methods used were identical with those described earlier (*4*) and were such as to give the total nitrogen, the total phosphoric acid, and the total potash present

in the leaf at the moment of sampling, irrespective of the form in which each was present.

PRESENTATION OF RESULTS

The plots with their treatments and yields are given in table 1.

The percentages of nitrogen, phosphoric acid, and potash in the fifth leaf from the base, at each date of sampling are shown in table 2, together with the intensities of nutrition and the composition of the NPK units. These data are shown graphically in the accompanying figures.

TABLE 1.—*Plot treatments and yields of fruit*

Plot No.	Treatment	N, P_2O_5, and K_2O equivalent applied to each plot	Symbol	Yield of fruit
		Grams		*Pounds*
10R	Nothing		O	88.1
10L	Manure		m	113.2
12L	Sodium nitrate	41.73	N	64.4
12R	Sodium nitrate+manure		N+m	121.9
14L	Superphosphate	125.19	P	43.3
14R	Superphosphate+manure		P+m	113.5
16L	Sodium nitrate + Superphosphate	41.73 + 125.19	NP	30.9
16R	Sodium nitrate + Superphosphate +manure		NP+m	117.9
18L	Sodium nitrate + Potassium chloride	41.73 + 43.10	NK	95.6
18R	Sodium nitrate + Potassium chloride +manure		NK+m	120.5
20L	Superphosphate + Potassium chloride	125.19 + 43.10	PK	98.8
20R	Superphosphate + Potassium chloride +manure		PK+m	129.3
2R	Sodium nitrate + Superphosphate + Potassium chloride	125.19 + 43.10	NPK	113.8
2L	Sodium nitrate + Superphosphate + Potassium chloride +manure		NPK+m	121.8
4R	Sodium nitrate + Superphosphate + Potassium chloride	83.46 + 125.19 + 43.10	(2N)PK	107.3
4L	Sodium nitrate + Superphosphate + Potassium chloride +manure		(2N)PK+m	115.5
8R	Sodium nitrate + Superphosphate + Potassium chloride	333.84 + 125.19 + 43.10	(RN)PK	104.5
8L	Sodium nitrate + Superphosphate + Potassium chloride +manure		(RN)PK+m	120.5

TABLE 2.—*The percentages of N, P_2O_5, and K_2O in the fifth leaf, their milligram-equivalent values, and the composition of the NPK-units at the three dates of sampling, for plants grown under different fertilizer treatments*

Date	Mineral content of dried foliage				Milligram-equivalent				Composition of NPK-units		
	N (M_x)	P_2O_5 (M_y)	K_2O (M_z)	$N+P_2O_5+K_2O$ s	N (E_x)	P_2O_5 (E_y)	K_2O (E_z)	S $E_x+E_y+E_z$	X $\left(100\times\frac{E_x}{S}\right)$	Y $\left(100\times\frac{E_y}{S}\right)$	Z $\left(100\times\frac{E_z}{S}\right)$
NOTHING (PLOT NO. 10R)											
	percent	*percent*	*percent*	*percent*							
April 5	3.960	1.871	1.495	7.326	282.744	79.143	31.843	393.730	71.811	20.101	8.087
April 29	2.900	2.500	.689	6.089	207.060	105.750	14.675	327.485	63.227	32.291	4.481
May 27	2.140	3.066	.646	5.852	152.796	129.691	13.759	296.246	51.577	43.778	4.644
MANURE (PLOT NO. 10L)											
April 5	3.960	1.346	3.630	8.936	282.744	56.936	77.319	416.999	67.804	13.653	18.542
April 20	2.880	1.746	1.906	6.532	205.632	73.856	40.597	320.085	64.243	23.074	12.683
May 27	2.140	1.833	2.067	6.040	152.796	77.535	44.027	274.358	55.692	28.260	16.047
N (PLOT NO. 12L)											
April 5	4.420	1.180	1.455	7.055	315.588	49.914	30.991	396.493	79.592	12.589	7.817
April 29	3.140	1.600	.835	5.575	224.196	67.680	17.785	309.661	72.404	21.856	5.740
May 27	2.520	1.840	.671	5.031	179.928	77.832	14.292	272..052	66.137	28.608	5.253
N+MANURE (PLOT NO. 12R)											
April 5	4.660	1.080	3.049	8.789	332.724	45.684	64.944	443.352	75.047	10.304	14.648
April 29	3.700	1.500	2.454	7.654	264.180	63.450	52.270	379.900	69.539	16.701	13.758
May 27	2.900	1.646	1.925	6.471	207.060	69.626	41.002	317.688	65.177	21.916	12.906
P (PLOT NO. 14L)											
April 5	3.900	1.886	0.852	6.638	278.460	79.778	18.147	376.385	73.983	21.196	4.821
April 29	2.380	2.386	.667	5.433	169.932	100.928	14.207	285.067	59.611	35.405	4.983
May 27	1.840	2.826	.646	5.312	131.376	119.540	13.760	264.676	49.614	45.183	5.202

P+MANURE (PLOT NO. 14R)											
April 5	3.680	1.013	3.490	8.183	262.752	42.850	74.337	379.939	69.156	11.278	19.566
April 29	2.600	1.673	1.698	5.971	185.640	70.768	36.167	292.575	63.450	24.187	12.361
May 27	2.180	1.746	1.647	5.573	155.652	73.856	35.081	264.589	58.827	27.913	13.268
NP (PLOT NO. 16L)											
April 5	4.440	1.473	1.137	7.050	317.016	62.308	24.218	403.542	78.559	15.438	6.001
April 29	2.740	1.920	.665	5.325	202.776	81.216	14.164	298.156	68.010	27.239	4.750
May 27	2.000	2.393	.594	4.987	142.800	101.224	12.652	256.676	55.634	39.436	4.929
NP+MANURE (PLOT NO. 16R)											
April 5	4.520	1.200	3.727	9.447	322.728	50.760	79.385	452.873	71.261	11.208	17.529
April 29	3.240	1.646	1.925	6.811	231.336	69.626	41.002	341.964	67.651	20.360	11.989
May 27	2.480	1.600	1.744	5.824	177.072	67.680	37.147	281.899	62.813	24.008	13.177
NK (PLOT NO. 18L)											
April 5	4.520	1.113	2.067	7.700	322.728	47.080	44.027	413.835	77.984	11.376	10.638
April 29	3.080	1.113	1.001	5.194	219.912	47.080	21.321	288.313	76.275	16.329	7.395
May 27	2.420	1.313	.775	4.508	172.788	55.540	16.507	244.835	70.573	22.684	6.741
NK+MANURE (PLOT NO. 18R)											
April 5	4.660	1.313	2.196	8.169	332.724	55.539	46.774	435.037	76.481	12.776	10.751
April 29	3.640	1.453	2.648	7.741	259.896	61.462	56.402	377.760	68.799	16.270	14.930
May 27	3.080	2.173	2.648	7.901	219.912	91.918	56.402	368.232	59.720	24.962	15.317
PK (PLOT NO. 20L)											
April 5	3.680	1.393	2.099	7.172	262.752	58.924	44.708	366.384	71.715	16.081	12.202
April 29	2.200	1.773	1.292	5.265	157.080	75.000	27.518	259.598	60.509	28.880	10.608
May 27	1.700	1.960	1.033	4.693	121.380	82.908	22.003	226.291	53.638	36.637	9.723

TABLE 2.—*The percentages of N, P_2O_5, and K_2O in the fifth leaf, their milligram-equivalent values, and the composition of the NPK-units at the three dates of sampling, for plants grown under different fertilizer treatments*—Continued

Date	Mineral content of dried foliage				Milligram-equivalent				Composition of NPK-units		
	N (M_x)	P_2O_5 (M_y)	K_2O (M_z)	$N+P_2O_5+K_2O$ s	N (E_x)	P_2O_5 (E_y)	K_2O (E_z)	S $E_x+E_y+E_z$	X $\left(100\times\frac{E_x}{S}\right)$	Y $\left(100\times\frac{E_y}{S}\right)$	Z $\left(100\times\frac{E_z}{S}\right)$
PK+MANURE (Plot No. 20R)											
April 5	4.260	1.300	4.166	9.726	304.164	54.990	88.736	447.890	67.910	12.277	19.812
April 29	3.020	1.686	2.680	7.386	215.628	71.319	57.084	344.031	62.676	20.730	16.592
May 27	2.300	1.920	2.196	6.416	164.420	81.216	46.774	292.210	56.199	27.793	16.006
NPK (PLOT NO. 2R)											
April 5	4.360	1.230	1.783	7.373	311.304	52.029	37.978	401.311	77.571	12.964	9.463
April 29	3.180	1.560	1.076	5.816	227.052	65.988	22.919	315.959	71.861	20.885	7.253
May 27	2.400	1.893	.826	5.119	171.360	80.074	17.594	269.028	63.695	29.764	6.539
NPK+MANURE (PLOT NO. 2L)											
April 5	4.360	1.184	3.727	9.271	311.304	50.083	79.385	440.772	70.627	11.363	18.010
April 29	3.200	.946	2.874	7.020	228.480	40.116	61.216	329.712	69.296	12.136	18.566
May 27	2.760	1.366	2.209	6.335	197.064	57.782	47.051	301.897	65.275	19.140	15.585
(2N) PK (PLOT NO. 4R)											
April 5	4.600	1.213	1.873	7.686	328.440	51.309	39.895	419.644	78.266	12.226	9.507
April 29	3.320	1.600	.981	5.901	237.048	67.680	20.895	325.623	72.797	20.785	6.417
May 27	2.720	2.153	.925	5.798	194.208	91.072	19.702	304.982	63.678	29.861	6.460
(2N) PK+MANURE (PLOT NO. 4L)											
April 5	4.540	1.240	2.842	8.622	324.156	52.452	60.534	437.142	74.153	11.998	13.847
April 29	3.460	1.480	2.704	7.644	247.044	62.604	57.595	367.243	67.269	17.046	15.684
May 27	2.800	1.386	1.563	5.749	199.920	58.628	33.292	291.840	68.503	20.089	11.407

(RN) PK (PLOT NO. 8R)											
April 5	4.820	1.226	2.164	8.210	344.148	51.859	46.093	442.100	77.843	11.730	10.425
April 29	3.880	1.320	1.309	6.509	277.032	55.836	27.881	360.749	76.793	15.478	7.728
May 27	3.080	1.640	.861	5.581	219.912	69.372	18.339	307.623	71.487	22.551	5.961
(RN) PK+MANURE (PLOT NO. 8L)											
April 5	4.620	1.233	3.081	8.934	329.868	51.156	65.625	446.649	73.853	11.453	14.692
April 29	3.780	1.280	2.667	7.727	269.892	54.144	56.807	380.843	70.866	14.216	14.916
May 27	3.220	1.260	2.357	6.837	229.908	53.298	50.204	333.410	68.956	15.985	15.057

DISCUSSION OF RESULTS

THE YIELDS FROM THE RESPECTIVE TREATMENTS

The order of yields in the unmanured series is not the same as that of the manured series. In the unmanured series the order in descending values is NPK>(2N) PK>(RN) PK>PK>NK> nothing> N>P>NP; and in the manured series PK+m>N+m>NPK+m> $\left\{\begin{matrix}\text{(RN) PK+m} \\ \text{and} \\ \text{NK+m}\end{matrix}\right\}$>NP+m>(2N) PK+m>$\left\{\begin{matrix}\text{manure} \\ \text{and} \\ \text{P+m}\end{matrix}\right\}$. In the unmanured series the four lowest yielding plots were those that received no potash. In the manured series the manure obscured, in general, the effects of an element added in the commercial fertilizer. Each element, however, increased the yields over the plot which received manure only. The highest yield resulted from the addition of potash and phosphate only, to manure. Increased quantities of nitrate in a complete fertilizer resulted in a reduction of yields in both the manured and unmaured plots.

THE GRAPHS SHOWING THE PERCENTAGES OF N, P_2O_5, AND K_2O AS ORDINATES AND DATES OF SAMPLING AS ABSCISSAE

Plots Without Manure

The nitrogen graphs (fig. 1) show that the nitrogen decreased progressively with increasing age of the leaves in all cases. At the first date of sampling, the nitrogen content of the leaves was higher in plants which received nitrate additions than in those that did not. The higher position of the graphs of the former indicates that this holds true for the whole cycle except in NP (plot No. 16L) during the latter part of the cycle.

The graphs for nitrogen are the highest and in increasing order in the leaves of plants which received twice the unit amount and biweekly unit additions of nitrogen, respectively. The fact that yields are in descending order the higher the graph, indicates that at the prevailing levels of phosphoric acid and potash, the buffer capacity of the plants for nitrogen has been exceeded in (RN) PK (plot No. 8R) and also in (2N) PK (plot No. 4R). But, beyond this, no relationship exists between the position of the nitrogen graphs and the yields from the various treatments.

The course of the graphs for phosphoric acid is abnormal, inasmuch as the graphs all slope upward with increasing age of the leaves, indicating progressively greater supply relative to demand of phosphoric acid with increasing maturity. The slope is least steep in the plot receiving biweekly additions of nitrogen (plot No. 8R) which shows that greater utilization of phosphoric acid has occurred. These facts suggest that nitrogen and phosphoric acid are out of physiological balance (*3*). The relationship is best considered from the viewpoint of the equilibrium between $N–P_2O_5–K_2O$ (pp. 823–826).

That this composted soil is very rich in phosphoric acid is indicated by the high content of the leaves of the check (nothing) plot (No. 10R) even at the first date of sampling. As a result, no relationship is apparent between the phosphoric acid content of the leaf and its presence in the fertilizer. Because of the greater accumulation of phosphoric acid with increasing age of the leaf in the lowest yielding plots, an inverse relationship of the phosphoric acid content of the leaves to yields exists. Moreover, except when accompanied

by nitrogen and potash, no relationship exists between the presence of phosphoric acid in the fertilizers and the yield.

The graphs for potash are abnormally low from all unmanured treatments. They are far below the nitrogen graphs throughout the cycle and even below those of phosphoric acid during the latter portion. The addition of potash is, however, reflected in the higher positions of the graphs of plants which received muriate. Moreover, the two lowest graphs for potash, NP (plot No. 16L) and P (plot No. 14L) are associated with the lowest yielding plots, and are fol-

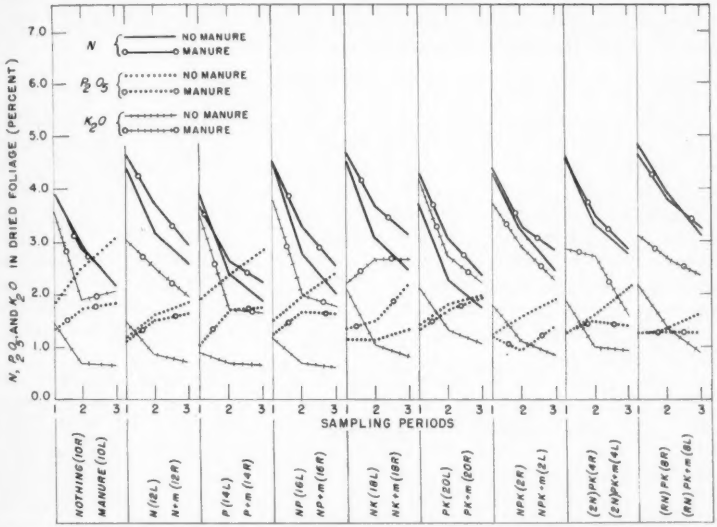

FIGURE 1.—Changes during the growth cycle in the content of N, P_2O_5, and K_2O in the fifth leaf resulting from the different treatments indicated with plot numbers in parentheses. Percentage values in terms of the dried foliage are given as ordinates, and dates of sampling as abscissae. The three dates of sampling (April 5, April 27, and May 29) are indicated by the digits 1, 2, and 3, respectively, along the base line.

lowed in order of yields and percentage of potash by the next two lowest yielding plots N (plot No. 12L) and check (plot No. 10R). In the unmanured plots there is, therefore, a relationship between the potash in the leaf and its presence in the fertilizer, between potash in the leaf and the yields, and between the presence of potash in the fertilizer and the yield.

THE MANURED PLOTS

The influence of nitrate additions is reflected also in the higher positions of the nitrogen graphs of the leaves from plants growing on the nitrated plots throughout the cycle. But no relationship exists between the height of a graph and the yield.

As in the unmanured series, no relationship exists between the phosphoric acid content of the leaf and its presence in the manure and mineral fertilizer.

At the first date of sampling, the potash content of the leaf is

highest in the highest yielding plot PK+m (plot No. 20R). But with this exception and contrary to the findings in the unmanured plots at this date, the influence of the mineral potash additions on the potash content of the leaf is masked by the influence of the potash in the manure. Thus, the K_2O content of the leaf in NP+m (plot No. 16R) is as high as that of NPK+m (plot No. 2L), and that of the check (nothing) is much higher than those of (2N) PK+m (plot No. 4L) and of (RN) PK+m (plot No. 8L). But with increasing maturity of the leaf, the influence of potash in the muriate is felt for in general, the graphs of the manured plots containing added mineral potash are less steep than of those of the unmanured plots and as a result, with one exception, end higher.

Comparison of the Graphs of the Manured and Unmanured Series

The nitrogen graph of plot 10L which received dressings of manure only coincides with that of the check plot, No. 10R. Furthermore, the nitrogen graphs of the manured complete-fertilizer plots (Nos. 4L and 8L) differ little from their respective unmanured plots (Nos. 4R and 8R), and the differences are not very great in P (plot Nos. 14L and 14R) except during the latter part of the cycle. However, relatively wide differences exist between the yields of the manured and the corresponding unmanured plot. In these treatments differences in the nitrogen content are not the factor causing differences in yields between the manured and its particular unmanured companion plot.

Greater differences between the graph of the manured and the corresponding unmanured plot are observed in N (plot Nos. 12L and 12R), NP (plot Nos. 16L and 16R), NK (plot Nos. 18L and 18R), and PK (plot Nos. 20L and 20R), in which the graph of the higher yielding manured plot is higher than that of the corresponding unmanured plot. In these plots, then, yields can be associated with differences in nitrogen content of the leaf.

With one exception, the graphs of phosphoric acid in the manured plots are below those of the corresponding unmanured plots. The exception is NK+m (plot No. 18R). The fact that manure dressings alone (plot No. 10L) have caused a reduction in the phosphoric acid content of the leaf much below that of the check or nothing plot (No. 10R), even at the first date of sampling, indicates that the seat of this inhibition lies in the soil, presumably, as the result of adsorption. The fact that little influence of the manure is observed in PK+m (plot No. 20R) throughout the cycle, and that the effect of the manure is small in the complete fertilizer plots at the early period, and is absent from NK+m (plot No. 18R) suggests that the forces causing the adsorption have been reduced by the addition of muriate of potash. The reduction in the phosphoric acid is associated with higher yields in the manured plots. But there is no evidence that differences in the content of phosphoric acid of the leaves of plants growing in the manured and unmanured plots, respectively, are a causal factor in producing the differences in yields. For example, wide differences in yields exist between a manured and its corresponding unmanured plot even when their graphs for phosphoric acid lie close together throughout the cycle.

The position of the lowest potash graphs for the manured plots is higher than that of the highest potash graphs for the unmanured

plots throughout the whole cycle, and, furthermore, the graph for potash of each manured plot is much higher than that of the unmanured plot throughout the whole cycle. The differences, moreover, are very much greater than those between the nitrogen graphs or the phosphoric acid graphs of any manured and unmanured pair. These facts suggest that with sufficiently high levels of nitrogen and phosphoric acid, potash is the determining factor that has produced these differences in yields between the manured and unmanured series. This relationship is best shown in the equilibrium between nitrogen, phosphoric acid, and potash considered later.

INTENSITIES OF NUTRITION AND EQUILIBRIUM BETWEEN NITROGEN, PHOSPHORIC ACID, AND POTASH AT SUCCESSIVE DATES OF SAMPLING

The graphs of figure 1 just discussed show in terms of the percentages of the dried foliage the relationship of supply of a particular element to demand by the plant for that element with increasing age of the leaf. They do not readily show, however, their physiological relationships to one another.

To show these relationships fully the percentages must be converted into milligram-equivalent values, arranged in such form as will indicate the equilibrium between nitrogen, phosphoric acid, and potash at each date of sampling. This has been done in the manner already described in earlier papers (*4*, *6*, *7*). In table 2, the values for X, Y, and Z in the last three columns represent the milligram-equivalent values for nitrogen, phosphoric acid, and potash, respectively, expressed as a combined NPK unit (*4*). This unit is derived by finding the proportion which each of the milligram-equivalent values shown in columns 10, 11, and 12 bears to the milligram-equivalent total. The values thus obtained are multiplied by 100 in order to avoid fractional magnitudes.

The analytical data obtained on samples collected on April 5 from the nothing plot (No. 10R) may be used to illustrate the method of calculating the NPK-unit.

Percent N $= M_x = 3.960$; percent $P_2O_5 = M_y = 1.871$; percent $K_2O = M_z = 1.495$.

Then $s = M_x + M_y + M_z = 7.326$, and

$$E_x = 1{,}000\frac{M_x}{N} = 71.4 \times 3.960 = 282.744$$

$$E_y = 1{,}000\frac{M_y}{1/6(P_2O_5)} = 42.3 \times 1.871 = 79.143$$

$$E_z = 1{,}000\frac{M_z}{1/2(K_2O)} = 21.3 \times 1.495 = 31.843$$

$$E_x + E_y + E_z = S = 393.730$$

$$X = 100 \times \frac{E_x}{S} = \frac{100 \times 282.744}{393.730} = 71.811$$

$$Y = 100 \times \frac{E_y}{S} = \frac{100 \times 79.143}{393.730} = 20.101$$

$$Z = 100 \times \frac{E_z}{S} = \frac{100 \times 31.843}{393.730} = 8.087$$

The values 71.811, 20.101, and 8.087 represent the values of the NPK unit of the fifth leaf taken April 5 from the check (nothing) plot.

The intensity of nutrition (s) consists of the sum of the percentages of nitrogen, phosphoric acid, and potash ($N+P_2O_5+K_2O$) at the moment of sampling a leaf and is shown in the fifth column of table 2.

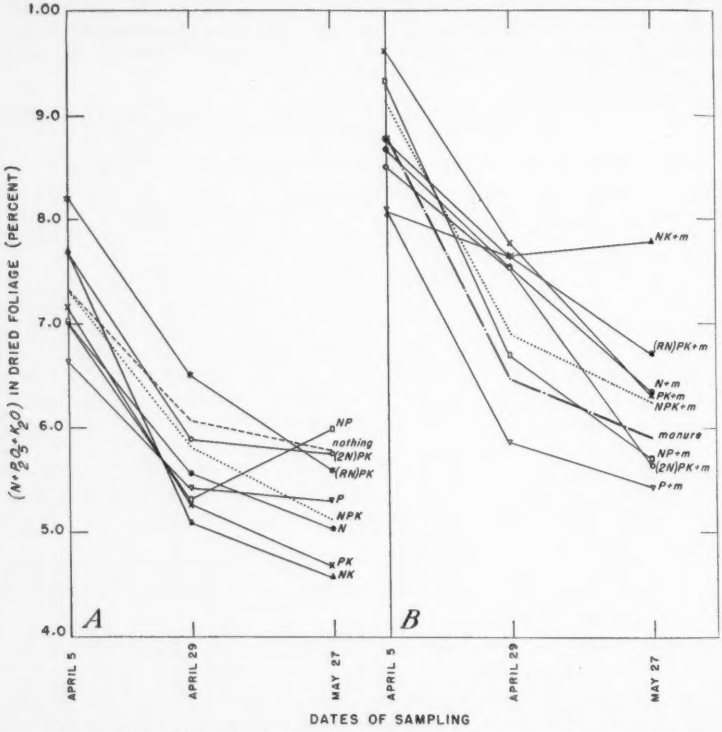

FIGURE 2.—Intensities of nutrition of the leaves at the three dates of sampling. Percentage values of $(N+P_2O_5+K_2O)$ in the dried foliage as ordinates and dates of sampling as abscissae: *A*, not manured; *B*, manured.

The method of foliar diagnosis has demonstrated that a fertilizer can be used intelligently only if it is selected with a knowledge of the manner in which it will affect the intensity, or the composition of the NPK-unit, or both simultaneously. The values for the intensities resulting from the various treatments with increasing age of the leaf are shown in figure 2, and the values for the physiological relations—the NPK-units—in trilinear coordinates in figures 3 to 6, inclusive.

THE INTENSITIES OF NUTRITION

In all treatments in the manured as well as in the unmanured series, except NK+m, Plot No. 18R, where a slight increase occurs in the last period, the intensities of nutrition decreased with increasing age of the leaf, in spite of the fact that one constituent (phosphoric acid)

of these magnitudes increased with increasing maturity of the leaf in all cases. This abnormal behavior of phosphoric acid did, however, modify the length and steepness of the slopes of figure 2 with increasing age of the leaf. This influence was especially noticeable in the unmanured plots. At the first date of sampling the lowest values for the intensities were associated with plots having the lowest yields, namely, P (plot No. 14L), NP (plot No. 16L), and N (plot No. 12L), and the highest value but one for the intensity with the treatment giving the highest yield, namely, PK+m (plot No. 20R). Furthermore, the intensity of the higher yielding manured plot was always higher than that of its unmanured companion plot. The intensity alone is not, however, the deciding factor in determining yields. It has been established by foliar diagnosis (*5*, *7*) that a low intensity of nutrition cannot compensate for a relatively good equilibrium between the elements, although a high intensity may compensate for a relatively poor equilibrium (*5*, *7*). So too, in the present experiment, the relatively low intensity of nutrition of the plot receiving manure only (plot No. 10L) resulted in the lowest yields of the manured plots, although the NPK equilibrium was relatively good.

The Equilibrium Between Nitrogen, Phosphoric Acid, and Potash

General Characteristics of the Graphs

The influence of the increase of phosphoric acid with increasing maturity of the leaves from all treatments, to which reference has already been made (p. 818), although affecting the intensities of nutrition but little, is reflected in the composition of the NPK-units. In figures 3 to 6 this is shown by the great displacements towards the right base apex representing $P_2O_5=100$ percent with increasing maturity of the leaf, and is especially noticeable in the unmanured plots. To conserve space in figures 3 to 6 only a part of the triangle, each side of which equals 100, is shown. On the other hand, the graphs of manured and unmanured plots alike, with increasing maturity, are displaced away from the summit of the triangle representing $N=100$ percent, indicating that the values for nitrogen in the NPK-unit decrease progressively with increasing age of the leaf. With two exceptions, the graphs for potash are displaced away from the apex representing $K_2O=100$ percent, indicating a decrease in the potash in the unit with increasing age of the leaf. The graph of each manured plot is displaced towards the left base apex in comparison with the graph of its unmanured companion plot, so that not only is the percentage of potash in the leaf of the manured plot higher (figure 1) but also its proportion relative to nitrogen and phosphoric acid in the NPK-unit is higher than that of the unmanured plot: The difference in the values for K_2O in the NPK-unit between any manured and unmanured pair is not less than 200 percent at any time.

Except in one case of manured and unmanured plots the graph of each manured plot is shorter than that of the unmanured one. And contrary to the relative positions of the nitrogen graphs of a manured and the corresponding unmanured plot in figure 1, based on the percentages of nitrogen in the dried material of the leaf, the trilinear coordinate graph of a manured plot is always displaced lower in the triangle at the first date of sampling than that of the unmanured one, indicating that in the former the proportion of nitrogen relative to

phosphoric acid and potash is less than in the latter. With increasing age of the leaf the displacement of the graph of a manured plot relative to that of the unmanured plot becomes less and less and in

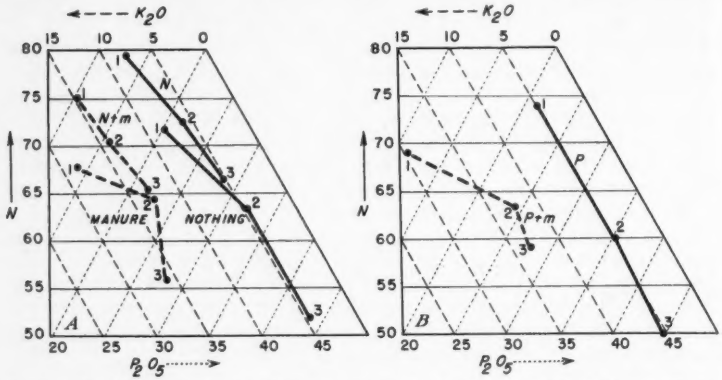

FIGURE 3.—Changes during the growth cycle in the N–P_2O_5–K_2O equilibrium in the fifth leaf from plants growing on: *A*, Plots No. 10R (nothing), No. 10L (manure), No. 12L (N), and No. 12R (N + manure); *B*, plots No. 14L (P) and No. 14R (P + manure). The composition of the NPK unit at the successive dates of sampling, April 5, April 27, and May 29, is indicated by the numerals 1, 2, 3, respectively.

most pairs is reversed during the later portion of the growth cycle. Accordingly, with increasing maturity the relative proportion of nitrogen in the NPK-unit is higher in the manured than in the unmanured

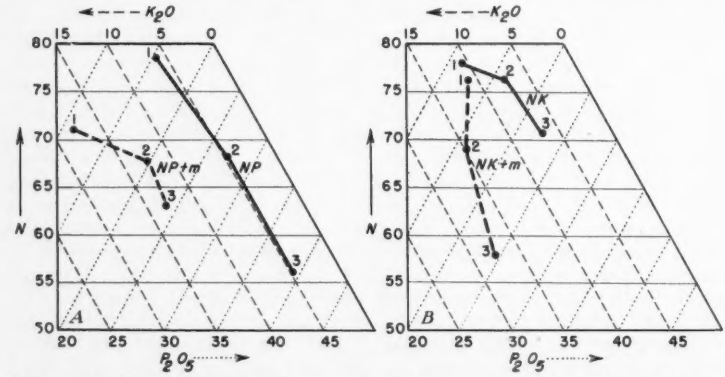

FIGURE 4.—Changes during the growth cycle in the N–P_2O_5–K_2O equilibrium in the fifth leaf from plants growing on: *A*, Plots No. 16L (NP) and No. 16R (NP + manure); *B*, plots No. 18L (NK) and 18R (NK + manure). The composition of the NPK unit at the successive dates of sampling, April 5, April 27, and May 29, is indicated by the numerals 1, 2, 3, respectively.

plot. Since in figure 1, little difference occurs between the forms and positions of the nitrogen graphs of the nothing and manure plots (Nos. 10R and 10L) and between (2N) PK and (RN) PK with their respective manured plots, the only possible conclusion is that the

fertilizer additions have made the nitrogen in the manure more available. This increased availability is masked in plots 4R and 4L and also in 8R and 8L by the increased additions of mineral nitrogen.

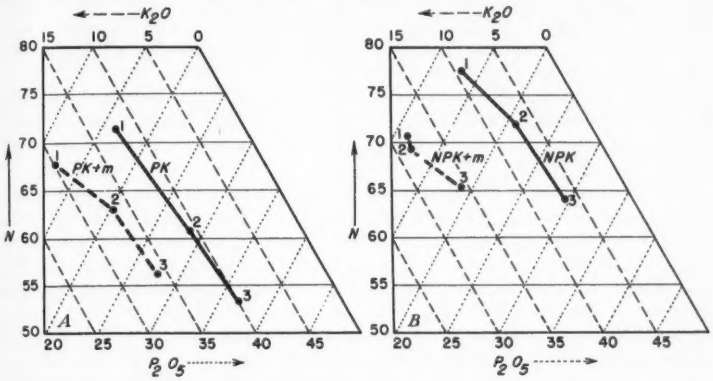

FIGURE 5.—Charges during the growth cycle in the N–P_2O_5–K_2O equilibrium in the fifth leaf from plants growing on: *A*, Plots No. 20L (PK) and 20R (PK + manure); *B*, plots No. 2R (NPK) and 2L (NPK + manure). The composition of the NPK unit at the successive dates of sampling, April 5, April 27, and May 29, is indicated by the numerals 1, 2, 3, respectively.

Except in one case, NK and the manured plot corresponding (plots 18L and 18R, fig. 6) the graph of each manured plot is displaced, relative to that of the corresponding unmanured one, away from the

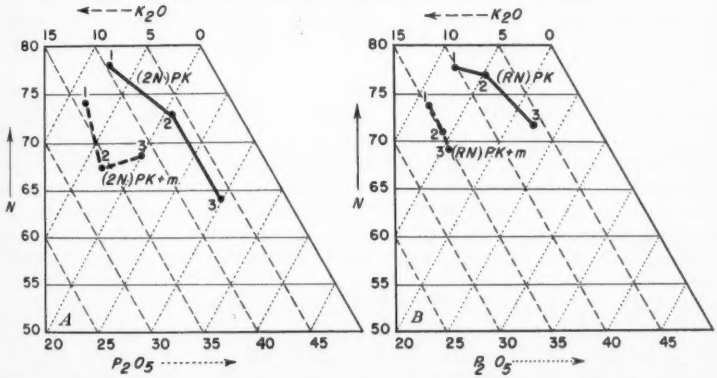

FIGURE 6.—Changes during the growth cycle in the N–P_2O_5–K_2O equilibrium in the fifth leap from plants growing on: *A*, Plots No. 4R ((2N)PK) and 4L ((2N)PK + manure); *B*, plots No. 8R ((RN)PK) and 8L ((RN)PK + manure). The composition of the NPK unit at the successive dates of sampling, April 5, April 27, and May 29, is indicated by the numerals 1, 2, 3, respectively.

right base apex throughout the cycle, indicating that the proportion of phosphoric acid in the NPK-unit has been reduced. In the NPK-units, then, the relationship between phosphoric acid of the manured and unmanured plots is not changed from that indicated in figure 1.

THE COURSE OF THE TRILINEAR COORDINATE GRAPHS DURING THE GROWTH CYCLE

In the *plots 10R (nothing) and 10L (manure)*, the relatively long and steep slope away from the summit (N=100 percent and towards the right base apex (P_2O_5=100 percent) of the check plot (No. 10R) indicates the rapid increase in phosphoric acid with increasing age of the leaf. This increase is made at the expense of the nitrogen and also of the potash (fig. 3, *A*).

The graph of manure (plot No. 10L) is shorter and is less steep than that of the nothing (plot No. 10R) and is displaced relative to it away from the right base apex (P_2O_5=100 percent) and towards the left base apex (K_2O=100 percent).

As compared with the graphs of plots 10R and of 10L, respectively, the graphs of the unmanured and manured plots Nos. 12L (N) and 12R (N+manure) (fig. 3, *A*), both of which received nitrate additions, are displaced toward the summit of the triangle and further away from the right base apex. This displacement indicates that the addition of nitrate of soda has resulted in an increase in the relative proportions of nitrogen, a reduction in the phosphoric acid, and not much change in the respective values for potash. Relative to the unmanured plot, the graph of the manured plot is displaced towards the left base apex, further away from the right base apex, and away from the summit of the triangle.

The forms of the graphs of the manured and unmanured plots Nos. 14L (P) and 14R (P+manure) (fig. 3, *B*), also Nos. 16L (NP) and 16R (NP+manure) (fig. 4, *A*), are very similar. The graphs of the unmanured plots are characterized by having the longest and steepest slopes towards the right base apex and away from the summit of any of the graphs, indicating that these treatments which have given the lowest yields are associated with the greatest reduction of nitrogen in the NPK-unit and with the greatest increase in phosphoric acid during the cycle, but with little change in the already very low values for potash.

The addition of nitrogen to phosphate is reflected in the displacement of the graph of 16L (fig. 4, *A*) towards the summit. The addition of manure has led to a reduction in the lengths of the graphs and in displacements toward the left base apex and away from the right base apex. At the first date of sampling, the graphs of the manured plots are displaced lower relative to the respective unmanured plots, but with increasing age of the leaf the relative displacements become less and less and are finally reversed in the latter part of the growth cycle.

Plots 18L (NK) and 18R (NK+manure) (fig. 4, *B*) are the only pair in which the graph of the unmanured plot is shorter than that of the corresponding manured one, indicating the exception to the findings in the other pairs that dressings of manure have reduced the relative proportion of phosphoric acid in the NPK-unit. In this pair the graph of the manured plot is below that of the unmanured during the whole cycle and not merely during the early portion.

As in other plots without nitrate additions the absence of this element is reflected in the positions and elongation of the graphs in plot Nos. 20L (PK) and 20R (PK+manure) (fig. 5, *A*). The graph of plot No. 20L is characterized by being nearer to the left base apex (K_2O=100 percent) than any of the manured plots during the whole cycle.

The similarity in lengths and positions of the graphs of the respective manured and unmanured plots Nos. 2R (NPK) and 2L (NPK+manure) (fig. 5, *B*); Nos. 4R ((2N)PK) and 4L ((2N) PK+manure) (fig. 6, *A*); and Nos. 8R ((RN) PK) and 8L ((RN) PK+manure) (fig. 6, *B*) is an indication that the addition of twice the unit amounts of nitrate of soda did not affect appreciably the proportions of nitrogen or of phosphric acid or of potash in the NPK-units. The graph of plot 8R relative to those of plots 2R and of 4R is shorter and is displaced higher in the triangle, indicating that biweekly additions of the

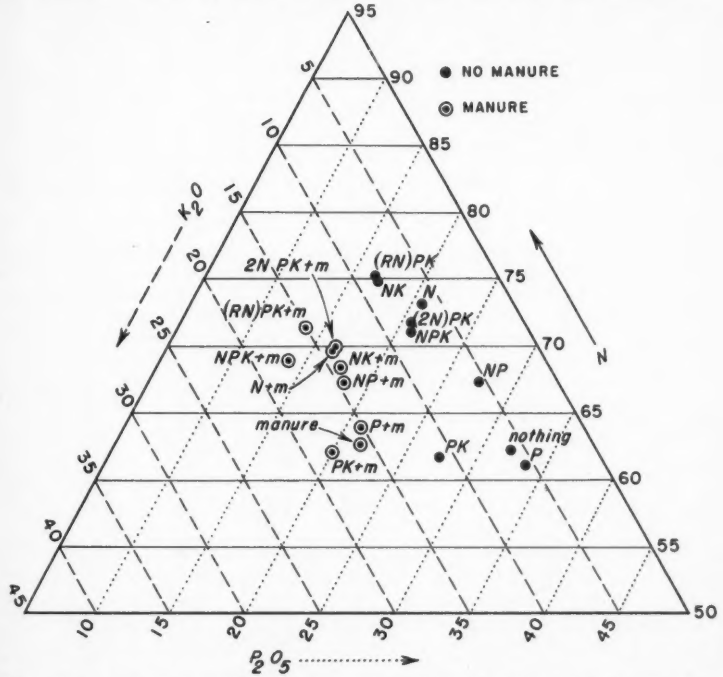

FIGURE 7.— Relative positions of the mean NPK-units of the fifth leaf from plants growing on the plots indicated. The mean NPK-unit represents the center of gravity of the respective graphs of figures 3 to 6, inclusive.

unit quantity of nitrate of soda has resulted in an increase in the proportion of nitrogen in the NPK-unit especially during the later stages of growth, a reduction in the phosphoric acid, and not much change in potash. The graphs of the respective manured plots are displaced towards the left base apex, away from the right base apex, and are lower in plot 8L throughout the cycle and in plots 2L and 4L during the early period.

THE MEAN INTENSITIES OF NUTRITION AND THE MEAN NPK-UNITS IN RELATION TO YIELDS

If yields are a measure of the practical results secured by a fertilizer, then the foliar diagnosis shows, as we have seen, the course of nutrition

with respect to the dominant fertilizer elements which determine these yields.

In relating yields to the foliar diagnosis, it is simpler to consider the resultant effects on the nutrition as indicated by values for the intensities and NPK-units, respectively, which are the means of the values at the different dates of sampling. When this is done the NPK-units can be represented by one point only, of which the absolute position on the triangle and the relative position with reference to the others are indicated at a glance.

Table 3 shows the mean of the values given in table 2 for the intensities and the composition of the NPK-units, respectively, at the several dates of sampling, in the case of each fertilizer treatment. These values are shown graphically in figure 7. By keeping in mind the fact that a fertilizer intervenes in the nutrition of a plant to affect (1) the intensity of nutrition or (2) the composition of the NPK-units, or both simultaneously, the data shown in table 3 can be analyzed from the point of view of the effects of the treatments on the mean intensity, or on the mean NPK-units, or on both simultaneously, and their relationship to the resulting yields.

TABLE 3.—*The mean intensities of nutrition, the mean NPK-units, and the yields of fruit on the various plots under different fertilizer treatments*

Plot No.	Treatment	Mean intensity of nutrition	Mean composition of the NPK unit			Yield of fruit
			N	P_2O_5	K_2O	
			Percent	*Percent*	*Percent*	*Pounds*
10R	Nothing	6.422	62.205	32.057	5.737	88.1
10L	Manure	7.169	62.579	21.662	15.757	113.2
12L	N	5.887	72.711	21.018	6.270	64.4
12R	N+manure	7.638	69.921	16.307	13.771	121.9
14L	P	5.794	61.069	33.928	5.002	43.3
14R	P+manure	6.576	63.811	21.126	15.065	113.5
16L	NP	5.787	67.401	27.371	5.227	30.9
16R	NP+manure	7.361	67.242	18.525	14.232	117.9
18L	NK	5.801	74.944	16.796	8.258	95.6
18R	NK+manure	7.937	68.333	17.999	13.666	120.5
20L	PK	5.710	61.954	27.199	10.844	98.8
20R	PK+manure	7.843	62.262	20.267	17.470	129.3
2R	NPK	6.103	71.042	21.204	7.752	113.8
2L	NPK+manure	7.542	68.399	14.213	17.383	121.8
4R	(2N)PK	6.462	71.580	20.957	7.461	107.3
4L	(2N)PK+manure	7.338	69.975	16.378	13.646	115.3
8R	(RN)PK	6.767	75.374	16.586	8.038	104.5
8L	(RN)PK+manure	7.833	71.225	13.885	14.888	120.5

THE UNMANURED PLOTS

As the result of the abnormal course of phosphoric acid with increasing age of the leaf no relationship exists between the mean values for the intensities and the yields of the unmanured plots. A relationship exists, however, between the mean values of the respective NPK-units and yields. Thus, the two lowest yielding plots NP (plot No. 16L) and P (plot No. 14L) are displaced the farthest from the left base apex, followed in order of position by the next lowest yielding treatments N (plot No. 12L) and check (plot No. 10R). The relatively small quantity of muriate added to each plot is reflected, therefore, by an increase in the K_2O of the NPK unit in the leaves of plants growing on the plots which received potash as muriate. With respect to the maximum yielding unmanured plots NPK (plot No. 2R) and

(2N)PK (plot No. 4R), the next lower in order of yields (RN) PK (plot No. 8R) and NK (plot No. 18L), have higher nitrogen and lower phosphoric acid. The next in descending order of yield, PK (plot No. 20L), has lower nitrogen and higher phosphoric acid. Of the four lowest yielding plots with lower potash, three also have lower values for nitrogen and two have higher values for phosphoric acid.

THE MANURED PLOTS

The influence of manure in reducing the accumulation of phosphoric acid with increasing age of the leaf, to which attention has already been called (p. 820), has resulted in a closer relationship between intensities and yields than is shown in the unmanured plots. Thus in the manured plots the four lowest yielding plots, manure (plot No. 10L), P+m (plot No. 14R), NP+m (plot No. 16R), and (2N)PK+m (plot No. 41) have the lowest mean values for intensities. In these manured plots high yields are associated with intensities of 7.54 or higher, and relatively low yields with intensities of 7.36 or lower. Although relatively high intensities thus are a necessary requisite for high yields, the determining factor in causing differences in yields among high yielding plots, however, must be looked for in the differences in the composition of the NPK-units. The highest yielding plot, PK+manure (plot No. 20R) has a mean NPK-unit in round numbers of 62.2 : 20.3 : 17.5. The next highest yielding plots, NPK+manure (plot No. 2L), N+manure (plot No. 12R), NK+manure (plot No. 18R), and (RN)PK+manure (plot No. 8L) have the following composition:

12R	69.9	16.3	13.8	Yield 121.9 pounds.
2L	68.4	14.2	17.4	Yield 121.8 pounds.
18R	68.3	18.0	13.7	Yield 120.5 pounds.
8L	71.2	13.9	14.9	

In these plots with somewhat lower yields than the optimum, the values for the nitrogen of the NPK unit are much higher than the optimum. This increase in the nitrogen has been made at the expense of both the phosphoric acid and potash in the N–P_2O_5–K_2O equilibrium, but principally at the expense of the latter. In the lowest yielding of the manured series having too low intensities, two, namely, P+m (plot No. 14R) and M (plot 10L), have too low potash relative to the optimum, and two, namely, (2N) PK (plot No. 4L) and NP (plot No. 16R), in addition to too low potash, have too high N and too low P_2O_5.

COMPARISON OF THE VALUES FOR THE MEAN INTENSITIES OF NUTRITION AND MEAN NPK UNITS OF THE MANURED AND UNMANURED PLOTS

In comparing the values for the mean intensities of nutrition and mean NPK units, it is to be noted that the higher yields of the manured over the unmanured plots, whether these received mineral fertilizers or not, are associated with higher mean intensities in the former. Moreover, as indicated in figure 7, the position of the mean NPK units of all the manured plots as a group is displaced relative to that of the unmanured plots towards the left base apex, indicating higher potash. They are also less scattered over the triangle than are those of the unmanured series. These facts indicate that the higher yielding manured plots as a group have higher mean intensities and a

greater relative proportion of potash in the NPK unit than the unmanured plots taken as a group. These generalizations hold also for the relationship of the mean intensity and the mean NPK unit of a particular treatment to that of its unmanured companion plot.

With one exception, a relationship also exists between the higher yields of the manured plots and the lower relative proportion of the mean value of the phosphoric acid in each of these plots respectively, as compared with the corresponding unmanured plots. But this exception may vitiate a casual relationship to yields. Considering the intensities and positions on the triangle of the NPK units (fig. 7) of the manured and unmanured series as a whole in relation to the optimum yielding plot, PK+m (plot No. 20R), the intensities of the unmanured series are too low and the positions of all the NPK units of the unmanured series lie too far from the left base apex, indicating too low potash. But beyond these characteristics, the manured and unmanured series show no other consistent relationship to yields.

Thus no consistent relationships relative to the summit (N=100 percent) of the triangle are observed between the position of the mean NPK units of the manured and unmanured plots as a group, or between the position of a manured plot and its unmanured companion. The proportion of nitrogen in the mean NPK unit, then, shows no causal relationship to yields. In fact, the third lowest value for N, viz, 62.26 of the highest yielding plot (PK+manure), must be regarded as sufficiently high for optimum yields. Similarly, differences in the proportion of phosphoric acid in the NPK unit show no consistent relation to yields.

SUMMARY

The method of foliar diagnosis has been applied to plants of the indeterminate type of growth, namely, tomatoes (*Lycopersicum esculentum* Mill.) grown under commercial greenhouse conditions.

The fertilizer treatments consisted of a single element, combinations of two elements, and also combinations of all three elements, nitrogen, phosphoric acid, and potash, with and without dressings of manure. The quantities of phosphoric acid and of potash in the commercial fertilizer remained unchanged in all treatments, but the quantity of nitrogen was varied in two cases. In the one double the standard unit amount was used, and in the other the unit quantity of nitrogen was added at biweekly intervals. In all cases the quantities of rotted horse manure added to the manured series remained unchanged.

The fifth leaf from the base of each plant was sampled at three different periods during the growth cycle and was analyzed according to prescribed methods.

The results of the analyses are recorded graphically by two methods, one indicating the relation of supply of an element to demand of the element by the plant with increasing age of the leaf in terms of percentages of the dried material, and the other by means of two magnitudes representing (1) the intensity of nutrition at the moment of sampling a leaf and (2) the physiological relationships between the elements also at the moment of sampling. The latter is shown in trilinear coordinates by means of a value designated the NPK unit, which represents the equilibrium between N, P_2O_5, and K_2O.

The order of yields in relation to the fertilizer treatment was not the same in the manured and unmanured series, respectively. In the

latter the highest yields resulted from the application of a complete fertilizer, while in the former from phosphate and potash without nitrate additions.

In both manured and unmanured series increased additions of nitrate of soda reduced yields below that from unit additions. The reduction in yields in both cases was associated with too high values for nitrogen, absolutely in terms of percentages in the dried foliage and also its proportion relative to phosphoric acid and potash in the composition of the NPK unit—values that exceeded the buffer capacity of the plant for this element at the prevailing levels of phosphoric acid and potash.

In the unmanured series the four lowest yielding plots were those which did not receive muriate of potash, and the foliar diagnosis showed that the leaves from the plants on the two lowest yielding plots had the lowest percentages of potash throughout the cycle. These plots were followed in order of yields and percentage of potash by the two other plots which did not receive any potash. Associated with the lowest yields were also the highest values for phosphoric acid throughout the cycle.

The relationships of foliar diagnosis to yields is most readily determined from the values representing the intensities of nutrition and the NPK units, respectively, and especially to the magnitudes representing their respective mean values.

In the unmanured series, because of far greater accumulation of phosphoric acid in some treatments than in others, a relationship existed between the intensity and the yield only at the first date of sampling. In these unmanured series, the highest yielding plots had the highest intensities of nutrition, and the lowest yielding the lowest intensities throughout the cycle.

In the unmanured series, the two lowest yielding plots were the furthest displaced from the left base apex where $K_2O=100$ percent, and were followed in position with respect to this apex by the two next lowest yielding plots.

High yields were associated with high values for the intensities of nutrition in the manured series and low yields with low values. In the manured plots having relatively high values for the intensities of nutrition but with yields lower than the optimum, the reduction in yields was associated with a much higher value for nitrogen in the NPK unit, made at the expense of the potash and also of the phosphoric acid, but principally of the former.

The lowest yielding plots in the manured series were associated not only with relatively low values for the intensities but also with too high a proportion of nitrogen in the NPK unit. In addition to too low values for nitrogen, in two cases [P+m] and [manure] the values for potash were found to be too low and those for phosphoric acid too high; and the two other low-yielding plots in the manured series [NP+m] and [(2N)PK+m] the values for phosphoric acid were too low.

The manured series of plots as a group gave higher yields than the unmanured series and each manured plot had a higher yield than the unmanured plot receiving a similar application of commercial fertilizer. Relative to these facts the foliar diagnosis shows that the increased yields of the manured over the unmanured plots as a group are associated with higher intensities of nutrition throughout the

cycle, and with a great increase in the potash of the NPK-unit, but with nitrogen and phosphoric acid showing no consistent relationships.

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EFFECT OF CERTAIN CHEMICAL ATTRIBUTES OF VEGETATION ON FOREST INFLAMMABILITY [1]

By LEON W. RICHARDS [2]

Cooperator, Northern Rocky Mountain Forest and Range Experiment Station, Forest Service, United States Department of Agriculture

INTRODUCTION

Forest Service administrators and fire-research men have long felt the need of information concerning the effect of vegetation such as shrubs, grasses, and forbs (nongrasslike herbs) on the rate of spread of fires. To date, all knowledge of the subject has been acquired empirically in the field, or deduced from knowledge of fire behavior as influenced by the condition of deadwood, duff, etc.[3] It is known that the luxuriant green vegetation of late spring and early summer does not lend itself to dangerous, fast-spreading fires, and that the matured and naturally cured or dried vegetation of September and October materially augments forest inflammability. Beyond this, the whole matter is one of conjecture. No information is available as to quantitative effects of forest undergrowth conditions on rate of fire spread, and no method has been evolved for determining readily and accurately whether these conditions at any particular time are such as would retard fire spread. Furthermore, little is known as to variation in volume of vegetation from season to season. Consequently, forest officers rating fire conditions and forecasting the approach of fire danger do not know what significance to assign to volume and condition of vegetation. Before fire danger can be properly rated on areas bearing large volumes of shrubs, grasses, and forbs, methods must be devised for evaluating these factors with reference to the spread of fire and for integrating data on these factors with measurements of the factors being utilized in fire-danger ratings at the present time—wind velocity and moisture content of dead fuels.

The problem of evaluating the effect of vegetation on rate of fire spread is fundamentally that of determining the heat-energy balance, that is, the ratio between the total heat energy available and the heat required to eliminate the moisture present, in whatever form. If the energy consumed in dissipating the plant moisture and bringing about combustion of the vegetative material is less than the energy produced by the combustion, the vegetation accelerates the spread of fire; if greater, the vegetation retards the spread.

The Northern Rocky Mountain Forest and Range Experiment Station, which has pioneered in the field of fire-danger rating, began, in 1935, studies of vegetation conditions in order to refine the methods of danger rating. The purpose of this work is to find measurable

[1] Received for publication December 16, 1939. The research reported here was conducted at the Priest River experimental forest of the Northern Rocky Mountain Forest and Range Experiment Station, U. S. Forest Service. This station's field of operations comprises a small portion of South Dakota, all of Montana, northern Idaho, and a portion of eastern Washington.

[2] Associate professor, Montana State University, employed during the summer months as a member of the Northern Rocky Mountain Forest and Range Experiment Station.

[3] HAWLEY, L. F. THEORETICAL CONSIDERATIONS REGARDING FACTORS WHICH INFLUENCE FOREST FIRES. Jour. Forestry 24: 756–763. 1926.

factors that will represent vegetation conditions throughout each fire season and to incorporate measurements of these factors into the scheme now being used to rate fire danger. The project is divided into three phases: Vegetation volume and appearance studies, dealing with current and total volume growth and visible physical changes that occur in the plants; chemical investigations; and test fires, which are essential for determining actual behavior of fires as affected by vegetation volume and condition. The first two phases should evolve a theory or hypothesis susceptible of being proved or disproved by the third. The physicochemical variations of certain typical plants as revealed by the exploratory work to date are described in this report.

The plants selected as typical of vegetative fuels on open forest areas of northern Idaho are: Shrubs, snowbrush (*Ceanothus velutinus*), ninebark (*Opulaster pauciflorus*), and willows (*Salix* spp.); grasses, downy chess or "cheatgrass" (*Bromus tectorum*) and pinegrass (*Calamagrostis* sp.); forb, fireweed (*Chamaenerion angustifolium*).

At the beginning of the chemical investigation, in 1935, the plan was to examine the vegetation with respect to moisture and fuel content, giving special attention to seasonal variations of both factors. It was assumed that the available fuel content could be represented by the crude fiber plus the crude fats or ether extractives, that is, the resins, waxes, and oils. The crude fats are of special interest because of their high inflammability. The crude fiber determinations were discontinued in 1936, because they had failed completely to show any significant variations corresponding to changes in fire behavior after the plants attained their structural growth. To determine more exactly the relation between the water content and the potential heat energy of vegetation, calorific determinations were begun in 1936. Moisture content, calorific value, and crude fat content were measured throughout the 1936 and 1937 fire seasons in one locality, the environs of the Priest River experimental forest in northern Idaho.

PROCEDURES AND RESULTS

In all cases, only green or curing material was collected; thoroughly cured portions were excluded. Of the shrubs only the leaves were used, but of the other plants the entire aerial portions.

A 500-gm. sample of each species was collected every 10 days throughout the summer season. The sampling was always done at 8 a. m., to reduce the effects of diurnal variations. Samples for moisture determination were sealed in moisture-proof cans and taken directly to the laboratory for weighing. The materials to be used in the crude fat and calorific determinations were allowed to dry on wire trays in a warm, well-ventilated room, then were ground to a powder and passed through a 60-mesh sieve.

Moisture content was determined by drying the materials in an oven at 105° C. until there was no further significant loss of weight. Results for the 1937 season are given in table 1.

A Parr peroxide bomb calorimeter was used satisfactorily in the calorific determinations. The size of the particles to which the oven-dried vegetation had been reduced insured complete combustion. The chemicals were passed through an 80-mesh sieve before use. Results for the 1937 season are given in table 2.

Total crude fat was determined by extraction with ether according to methods outlined by the Association of Official Agricultural Chemists.[4] Results for the 1937 season are given in table 3.

TABLE 1.—*Percent of moisture*[1] *in vegetation of open forest areas as determined at 105° C. in 1937*

Species[2]	June 20	June 30	July 10	July 20	July 30	Aug. 10	Aug. 20	Aug. 30	Sept. 10
Snowbrush	215	212	191	177	165	146	131	120	112
Ninebark	197	218	206	148	160	137	115	101	109
Willows	230	235	183	162	156	137	123	120	113
Downy chess[3]	150	116	24	9					
Pinegrass	182	176	160	152	138	129	118	107	110
Fireweed	426	341	305	290	294	257	244	249	241

[1] All values were calculated on the basis of oven-dry weight of single samples, checked by 2 or more similar determinations made in the course of other phases of this project.
[2] The snowbrush sample was composed of leaves of various ages in proportion to those on the plant. For ninebark and willows, leaves of the current year only were collected. For downy chess, pinegrass, and fireweed, the entire aerial portion (current year's growth) was used.
[3] On July 30 and later no green growth was present.

TABLE 2.—*Calories per gram, on basis of oven-dry weight,*[1] *determined on vegetation of open forest areas in 1937*

Species	June 20	June 30	July 10	July 20	July 30	Aug. 10	Aug. 20	Aug. 30	Sept. 10	Average
Snowbrush	4,600	4,800	4,900	5,000	5,000	5,000	5,100	5,200	5,200	4,990
Ninebark	[2] 5,000	4,500	4,600	4,600	4,700	4,800	4,700	4,600	4,700	4,690
Willows	4,600	4,800	4,800	4,800	4,700	4,700	4,700	4,700	4,800	4,730
Downy chess[3]	4,300	4,300	4,400	4,300						4,330
Pinegrass	4,200	4,000	4,100	3,900	3,900	4,100	4,000	3,900	3,800	3,990
Fireweed	4,300	4,300	4,300	4,400	4,400	4,400	4,400	4,400	4,400	4,360

[1] All determinations were computed to an accuracy of 1 calorie per gram, but for the sake of comparison the figures are rounded off to the nearest hundred. Each tabulated value is the average of 2 determinations agreeing within 30 calories.
[2] Probably affected by a sampling error.
[3] On July 30 and later, no green growth was present.

TABLE 3.—*Percent of crude fat*[1] *in vegetation of open forest areas, 1937*

Species	June 20	June 30	July 10	July 20	July 30	Aug. 10	Aug. 20	Aug. 30	Sept. 10
Snowbrush	5.3	7.2	7.0	7.6	9.2	12.8	11.2	10.5	11.8
Ninebark	[2] 7.2	3.7	5.7	5.5	6.6	7.1	6.5	6.4	7.3
Willows	5.7	6.4	6.1	6.0	6.6	6.6	6.7	6.0	6.2
Downy chess[3]	2.5	2.6	3.3	2.2					
Pinegrass	4.4	3.4	4.1	3.6	4.0	5.2	4.8	5.0	5.8
Fireweed	4.0	4.2	3.4	4.3	5.1	6.0	5.5	5.7	6.8

[1] Averages of 2 determinations.
[2] Possibly affected by a sampling error.
[3] On July 30 and later, no green growth was present.

DISCUSSION

Before considering the data, it should be pointed out that climatically the growing season of 1937 at the Priest River experimental forest was exceptional. The month of May was the driest recorded in 25 years of observation, and both April and June were the wettest on record. July precipitation, although not establishing a record,

[4] ASSOCIATION OF OFFICIAL AGRICULTURAL CHEMISTS. OFFICIAL AND TENTATIVE METHODS OF ANALYSIS . . . Ed. 2, 417 pp., illus. Washington, D. C. See p. 72.

was well above average,[5] and that of August was 31 percent below average.

Plant moisture content undoubtedly plays the major role in the influence of vegetation conditions on rate of fire spread, as was suggested by Hawley's conclusions. Moisture content varies widely, not only seasonally for each species but also on the same date among different species growing side by side (table 1). Especially noteworthy are the data for downy chess and fireweed. The former, which cures very early, was definitely inflammable early in July. Collections of downy chess were discontinued after July 20, because all green color had disappeared and the sample plants were definitely cured. In this state, with only 9 percent of moisture, each gram of this cured material was found capable of producing 3,900 calories to contribute to the spread of fire. Fireweed, in contrast, registered at the end of the season, September 10, a moisture content of 241 percent, which is higher than that of any of the other plants of this group when they were wettest, and on June 20 and 30. With its fuel value of nearly 4,400 calories per gram and moisture content of 241 percent, this plant was capable of producing only 1,300 calories per gram on complete combustion. It is conceivable that, 71 percent of its composition being water, fireweed continues even at the end of the season to exert a retarding effect on the spread of fire.

Observations on test fires in 1935 and 1936 indicated entirely different reactions and burning properties for snowbrush, ninebark, and willows, although the moisture content and calorific values of the plants at the time were similar. As had previously been noted by trained field observers while on actual fires and test burns, the willows exhibited superior fire resistance. At any one time during the 1937 season the differences in water content of snowbrush, ninebark, and willows were not large, never as much as 20 percent (table 1).

This raised the question of the relative tenacity with which plants of different species hold their moisture when subjected to fire. The rate of loss of water might, for instance, be significantly influenced by the fact that part of the water content of green plants is colloidally bound. Evaporation tests were therefore undertaken specifically to determine the rate of water loss at moderately high temperatures. On September 10, by using a temperature of 170° C. and weighing the samples every half hour, it was found that loss of moisture in the first 30 minutes amounted to 48 percent of total moisture content for freshly picked green leaves of snowbrush, as against 38 percent for similar samples of ninebark and only 32 percent for willow. At a temperature of 170° C., morphological differences of the leaves cannot account for the differences noted in rate of loss of moisture. What, then, are the water-retention forces involved, and how can the energy necessary to overcome these forces be measured? An effort is being made to extend the present study to include an investigation of the nature of the plant juices as a possible partial explanation.

According to the calorific determinations in table 2, only snowbrush and pinegrass varied markedly during the season in total or potential heat energy, the former exhibiting a small gain, the latter a mid-season dip, a recovery, and then a late-season decline. The mid-

[5] The exceptional wetness of April, June, and July offers a possible explanation of some significant results of the vegetation volume phase of this study. According to the volume measurements, based on oven-dry weight, the plants made 50 percent more total growth in 1937 than in either 1935 or 1936, seasons with rainfall slightly below the mean.

season dip of the pinegrass probably was due to sampling technique, which until after July 30 did not eliminate the possibility of collecting samples from plants that had previously been clipped. The August 10 to September 10 data are believed to indicate the true condition of the species.

The 600-calorie increase noted in snowbrush would seem to be a significant gain in available energy that should cause a marked difference in the fire behavior of this plant as the season progressed. The concurrent decrease of moisture represents a further increase in available heat energy. For example, 1 gm. of the fresh green plant in the field on June 20 contained 0.68 gm. of water and 0.32 gm. of solid material, representing only 1,400 calories. On September 10, 1 gm. of this same plant contained 0.53 gm. of water and 0.47 gm. of solid matter, representing 2,400 calories. The increase of 1,000 calories per gram is possibly significant from the standpoint of the fuel energy/water content relation.

From the information available at present, the quantity of energy necessary to rid living vegetation of its water can be only roughly approximated. On the basis of the thermal capacity of free water, the heat of vaporization, and the specific heat of water vapor, it is estimated that to dissipate the 0.68 gm. of water contained in each gram of green snowbrush on June 20 would require approximately 500 calories. On this same basis, it is estimated that to dissipate the 0.53 gm. of water in the snowbrush on September 10 would require roughly 350 calories. When this decrease from 500 to 350 calories is considered in relation to the concurrent increase of 1,000 calories per gram of green vegetation, it is obvious that the potential rate of spread of fire through snowbrush brush fields should be expected to increase between June 20 and September 10.

As a rule the calorific values of the crude fats are considerably higher, and their ignition temperatures are measurably lower, than those of cellulose. Any significant change in either quantity or nature of these constituents might readily alter the burning properties of the plants. Particularly is this the case for snowbrush, which has been provided by nature with a liberal covering of oleaginous material on the upper surface of the leaf. The crude fat data obtained in these examinations (see table 3) are of interest not only because of the seasonal variations indicated in the quantity of these materials and the relatively large proportion of the total weight that they constitute, but also because of the differences and similarities evidenced between species.

To date, no effort has been made to ascertain the nature of the constituents making up the crude fats. It is conceivable that the continued increase in the calorific value of snowbrush after August 10, despite the crude fat decrease, may be due to a change in the nature of the fats. An increase in the hydrocarbon fraction of the volatile oils would tend to increase calorific values and also introduce an additional danger factor, that of lower ignition temperatures due to increased ease of vaporization. Therefore, it would seem advisable to include this phase in future considerations.

CONCLUSIONS

Quantitative variations in the moisture content of the vegetation on this area in the northern Rocky Mountains appear to exert the

dominant influence on the fire behavior of the plants through the fire season. Moisture content of plants of each of the species studied varied widely, and in some cases wide differences in moisture content were exhibited by neighboring plants of different species. In all the species, a decided decrease in moisture content took place as the season advanced; undoubtedly, this decrease is the principal cause of increased inflammability. As critical fire conditions develop, factors other than total free moisture may gradually assume increased importance. The tenacity with which a given plant holds its free or chemically combined moisture may determine whether it exerts a retarding effect, no effect, or an accelerating effect on the rate of spread of forest fires. As yet insufficient data are at hand to permit any conclusions to be drawn concerning the significance of calorific variations. At present it is impossible to estimate, for example, in any but the most general way, what effect an increase of 600 calories per gram would have on rate of spread.

THE EFFECT OF ALKALINE DUST DILUENTS ON TOXICITY OF ROTENONE-BEARING ROOTS AS DETERMINED BY TESTS WITH HOUSEFLIES [1]

By T. C. ALLEN, *assistant professor of economic entomology*, and J. W. BROOKS, *assistant in economic entomology, Wisconsin Agricultural Experiment Station* [2]

INTRODUCTION

Little information appears to be available regarding the effect of dust diluents on the toxicity of rotenone-bearing plant insecticides. The knowledge that rotenone is deteriorated by alkalies under laboratory conditions has been reported by Jones and Haller [3] and Takei, Miyajima, and Ono.[4] Under field conditions, Walker and Anderson [5] and others have shown that rotenone-bearing roots mixed with alkaline dust diluents are not as effective as those diluted with neutral or acid carriers. As a result, during the past few years, alkaline diluents such as hydrated lime have been discontinued as carriers for rotenone bearing insecticides, and substitute carriers such as clay, talc, gypsum, sulfur, and many other materials have been recommended. Further knowledge of the losses in toxicity of ground rotenone-containing roots when associated with highly alkaline materials is of major importance for the proper preparation of dust insecticides.

In preliminary reports by the authors [6] the hydrogen-ion potential of several rotenone-bearing dust insecticides was given. The pH values of these preparations, obtained by the colorimetric, the quinhydrone, and the glass electrode methods, showed that dust diluents range from pH 4.23, in the case of calcium sulfate, to approximately pH 12.55, in the case of hydrated lime. Toxicity tests of these dusts on cabbageworms indicated that a possible relation existed between the hydrogen-ion concentration of the dust mixture and its toxicity to insects. Since a large percentage of the insecticidal dusts are alkaline a detailed study of the effect of alkalinity upon rotenone-bearing dusts was made by testing kerosene extracts of the dust mixtures on houseflies (*Musca domestica* L.).

MATERIALS AND METHODS

The materials used in these studies included a group of dust diluents such as are frequently employed in dust insecticides, and three types of rotenone-bearing plants. In selecting the dust diluents for testing purposes, care was taken to employ representative samples of dusting materials which varied widely in hydrogen-ion potential. The rote-

[1] Received for publication October 20, 1939.
[2] The writers wish to express their appreciation to Dr. Churchill Eisenhart for the presentation of the statistical data.

[3] JONES, HOWARD A., and HALLER, H. L. THE "YELLOW COMPOUNDS" RESULTING FROM THE DECOMPOSITION OF ROTENONE IN SOLUTION. Amer. Chem. Soc. Jour. 53: 2320–2324. 1931.

[4] TAKEI, SANKICHI, MIYAJIMA, SHIKIRO, and ONO, MINORU. ÜBER ROTENON, DEN WIRKSAMEN BESTANDTEIL DER DERRISWURZEL, XI. ROTENONHARZ. QUANTITATIVE BESTIMMUNG DES ROTENONS UND DES DEGUELINS IM ROTENONHARZ. Deut. Chem. Gesell. Ber. 66: 1826–1833. 1933.

[5] WALKER, HARRY G., and ANDERSON, LAUREN D. NOTES ON USE OF DERRIS AND PYRETHRUM DUSTS FOR THE CONTROL OF CERTAIN INSECTS ATTACKING CRUCIFEROUS CROPS. Jour. Econ. Ent. 27: 388–393, illus. 1934.

[6] CLARK, NOBLE, compiler. ALKALINE CARRIERS REDUCE EFFECTIVENESS OF DERRIS FOR CABBAGEWORMS, Wis. Agr. Expt. Sta. Bul. 438: 124. 1937.
—— ALKALINE CARRIERS INJURE ROTENONE. Wis. Agr. Expt. Sta. Bul. 443: 47. 1939.

none-bearing roots which were mixed with these diluents were obtained from three different sources: Derris (*Derris eliptica*) was an import from the Malayan Peninsula; timbo (*Lonchocarpus* sp.) was obtained from Brazil; and barbasco (*Lonchocarpus* sp.) from Peru. Analyses[7] of these roots showed the derris to contain 5.9 percent of rotenone and 14.72 percent of total ether extractives; the timbo, 5.0 percent of rotenone and 20.3 percent of total ether extractives; and the barbasco, 4.55 percent of rotenone and 16.0 percent of total ether extractives.

The diluents chosen for use in the testing varied in respect to both pH value and chemical nature. The dihydrate calcium sulfate and the powdered magneisum carbonate were chemically pure products. The kaolin, gypsum, talc, and hydrated lime were commercial products, as was the 99½ percent pure dusting sulfur. The tobacco filler, also a commercial product, was derived from byproducts of the tobacco industry.

The dusts employed for testing purposes were prepared by mixing 1 part of the rotenone-bearing root with 9 parts of the diluent. Preparations were made with derris, timbo, and barbasco in the same proportions with each diluent to be tested. The derris samples mixed in this manner contained 0.59 percent of rotenone, and 1.47 percent of total ether extractives. The timbo dust mixtures contained 0.5 per cent of rotenone and 2.03 of total ether extractives, while the barbasco mixtures contained 0.45 percent of rotenone and 1.6 of total ether extractives. Replicate tests were conducted with each of the above rotenone-bearing plants.

Before the toxicity tests, the dust mixtures were moistened with distilled water, placed in storage at room temperature, and kept there without light for 7 days The storage period provided conditions for possible deterioration of the dust samples. Replicate unmoistened samples used as checks were stored in the dark for a similar period.

The hydrogen-ion concentration of the various moistened and unmoistened dust preparations was determined by the glass electrode method. The procedure used in determining the pH values was similar to that employed in determining the pH values of soil samples. A measured amount of the dust mixture was placed in a vial with a definite amount of distilled water. This solution was agitated a fixed number of times and allowed to remain in the vial for 1 hour. The solution was then poured into the testing cup of the glass electrode indicator and the pH value recorded. Three readings were taken and the average was recorded as the pH value of the sample. The readings were made over a 1-, 3-, 5-, and 7-day period. The dusts were then thoroughly dried, repowdered, and passed through a 100-mesh screen before being used for testing purposes.

A modification of Campbell's settling mist method [8] for testing the relative toxicity of contact insecticides against houseflies was employed in determining the relative toxicity of the various dust preparations. Five-day-old flies were subjected to a settling mist of kerosene containing an extract of the various dusts. The extracts were prepared by steeping 10 gm. of the dust in 20 cc. of oil at room temperature for 24 hours. The "steepate" was then filtered and the filtrate tested immediately against the houseflies. For each test,

[7] Determined by John Powell & Co.

[8] ZERMUEHLEN, A. E., and ALLEN, T. C. TESTING FLY SPRAYS. MODIFIED PROCEDURE IN TESTING PETROLEUM BASE INSECTICIDES BY THE SETTLING MIST METHOD. Soap 12 (6): 105-107, illus. 1936.

2.5 cc. of the filtrate was atomized into the bell jar under 25 pounds pressure. The length of the exposure period was 2 minutes. Mortality records were taken over a period of 3 days. Flies subjected to a mist of kerosene and to kerosene extracts of diluents which did not contain rotenone-bearing plant materials were used as checks.

RESULTS

The pH values of a number of carriers for insecticidal dusts are shown in table 1. These determinations indicate that there is considerable variation in reaction among dust carriers. The samples of ground rotenone-bearing roots employed in these tests showed pH values on the acid side, and all samples were quite similar in reaction although the roots were obtained from widely different sources.

Moist rotenone-bearing roots both with and without the diluents were stored in the absence of light for a period of 7 days. The moisture content of these dusts was maintained at approximately 48 percent by weight through daily additions of water during the storage period. The absorption of moisture varied with respect to the hygroscopic properties of the diluent under consideration. There was considerable change in the pH values of the rotenone-bearing roots both with and without the diluent (table 2).

Under laboratory conditions, moist stored dusts commonly produced growth of various micro-organisms. Presumably rapid fermentation processes occurred in these samples as a result of the presence of carbohydrates in the ground roots of the plants. Acidity which accompanied fermentation was due no doubt to the formation of certain organic acids, such as acetic and malic acid. Sugar determinations of derris, timbo, and barbasco roots showed that sufficient carbohydrates were present to account for the rapid fermentation of the stored samples. The hydrogen-ion concentration of sterilized samples of these roots remained unchanged standing, and no apparent growth of micro-organisms occurred during the storage period.

TABLE 1.—*The approximate pH values of various dust diluents and rotenone-bearing roots as determined by glass electrode indicator*

Material[1]	pH	Material[1]	pH
Calcium sulfate	4.23	Talc A	8.24
Clay A	4.30	Talc B	8.30
Pyrethrum flowers	4.57	Clay J	8.36
Kaolin	4.76	Copper carbonate	8.45
Walnut shell flour	5.09	Talc C	8.59
Clay B	5.13	Bentonite	8.64
Tobacco dust	5.92	Infusorial earth	8.66
Pyrophyllite	6.19	Calcium carbonate A	8.71
Clay C	6.23	Ammonium carbonate	8.76
Plaster of paris	6.35	Calcium carbonate B	9.32
Clay D	6.40	Diatomaceous earth	9.63
Sulfur (flowers)	6.46	Magnesium carbonate A	9.78
Rare rock phosphate	6.50	Gypsum B	9.93
Clay E	6.54	Sodium carbonate	10.90
Gypsum A	6.57	Magnesium carbonate B	10.93
Clay F	6.60	Calcium carbonate C	11.10
Clay G	6.84	Tobacco filler	11.80
Sodium bicarbonate	7.50	Hydrated lime	12.50
Clay H	7.66	Derris	6.30
Clay I	8.03	Timbo	6.55
Distilled water	6.45	Barbasco	6.57

[1] Symbols represent products of different trade names.

TABLE 2.—*Effect of damp storage for 7 days upon the hydrogen-ion concentration of various rotenone-bearing roots with and without dust diluents*

Dust samples[1]	pH of moist samples after—				
	1 hour	1 day	3 days	5 days	7 days
Derris	6.30	6.16	5.65	5.05	4.95
Timbo	6.55	5.65	4.23	4.06	4.08
Barbasco	6.57	5.91	4.60	4.15	4.12
Derris-calcium sulfate	7.50	7.00	7.20	7.04	6.90
Timbo-calcium sulfate	7.15	6.85	6.25	5.31	5.20
Barbasco-calcium sulfate	6.85	6.50	5.70	4.24	4.12
Derris-kaolin	8.00	7.46	7.25	6.32	6.28
Timbo-kaolin	8.50	7.78	7.45	6.40	5.81
Barbasco-kaolin	8.30	7.30	7.35	6.45	6.15
Derris-sulfur	6.60	6.35	5.82	5.38	5.10
Timbo-sulfur	6.56	5.77	4.55	4.00	3.82
Barbasco-sulfur	6.60	5.81	4.74	4.35	4.22
Derris-gypsum	6.00	6.05	5.73	5.48	5.30
Timbo-gypsum	6.15	5.76	5.15	4.17	3.98
Barbasco-gypsum	6.17	5.90	5.11	4.15	4.05
Derris-talc	8.90	8.98	7.60	7.11	7.36
Timbo-talc	9.00	8.70	7.35	7.30	6.92
Barbasco-talc	8.88	8.20	7.32	6.82	6.30
Derris-magnesium carbonate	10.20	10.05	10.00	9.80	9.52
Timbo-magnesium carbonate	10.10	9.80	9.78	9.45	9.23
Barbasco-magnesium carbonate	10.00	9.75	9.50	9.30	9.15
Derris-tobacco filler	11.85	11.85	11.70	11.76	11.69
Timbo-tobacco filler	11.83	11.81	11.72	11.75	11.78
Barbasco-tobacco filler	11.88	11.75	11.75	11.73	11.72
Derris-hydrated lime	12.50	12.50	12.50	12.50	12.47
Timbo-hydrated lime	12.52	12.50	12.48	12.42	12.50
Barbasco-hydrated lime	12.55	12.51	12.49	12.48	12.49

[1] 9 parts of diluent to 1 part of rotenone-bearing roots.

Fermentation and consequent formation of acids did not occur in the highly alkaline samples. This finding was confirmed in part by observations for perceptible growth of microflora and by pH determinations, which showed no change during the storage period. The acid dust mixtures, however, were a favorable medium for the development of micro-organisms, and in these samples there was a tendency for acids to form. From these results it appears that the acid dust preparations in which greater activity of micro-organisms occurred, tended to retain their toxicity to houseflies. This is contrary to the reports of some workers that micro-organisms present in stored derris solutions are responsible for the deterioration of the toxic ingredients.

In some instances, the final dust mixtures (tables 1, 2, and 3) had pH values greater than those of either the rotenone-bearing material or the diluent. This may be due to some reaction between the diluent and the ground root when they are in an aqueous medium. In such reactions more hydroxyl-ions may be liberated, giving rise to a more alkaline reading.

To determine approximately the minimum quantity of moisture that would bring about a deterioration in the toxicity of the insecticides, further tests were made. Four representative dust samples were dried, three replicates of each sample weighed, placed in a constant temperature-humidity chamber at 73° F. and 61 percent relative humidity, and kept there for 7 days. The samples were then removed from the chamber and reweighed to determine the amount of moisture absorbed. The moisture content of the different samples ranged from 0.3 to 9.7 percent. When oil filtrates of these samples were tested on houseflies, the alkaline samples showed a deterioration quite similar to that of the alkaline samples in table 3, in which the samples contained approximately 48 percent of moisture.

TABLE 3.—*Percentage kill of houseflies by kerosene extracts of derris, timbo, and barbasco dust mixtures, when tested following a 7-day period in damp storage*

Rotenone-bearing dust [1]	pH	Tests made	Flies tested	Flies killed		Average kill
		Number	*Number*	*Number*	*Percent*	*Percent*
Derris-sulfur	6.60	6	274	273	99.6	99.2
Timbo-sulfur	6.56	6	257	254	98.8	
Barbasco-sulfur	6.60	6	262	260	99.2	
Derris-gypsum	6.00	6	239	239	100.0	97.4
Timbo-gypsum	6.15	6	265	260	98.1	
Barbasco-gypsum	6.17	6	261	246	94.2	
Derris-buffer [2]	6.57	6	285	278	97.6	96.0
Timbo-buffer [2]	6.57	6	268	246	91.8	
Barbasco-buffer [2]	6.57	6	273	269	98.5	
Derris-calcium sulfate	7.50	6	249	212	85.1	90.2
Timbo-calcium sulfate	7.15	6	240	226	94.1	
Barbasco-calcium sulfate	6.85	6	269	246	91.4	
Derris-talc	8.90	6	244	59	24.1	35.0
Timbo-talc	9.00	6	252	117	46.4	
Barbasco-talc	8.88	6	229	78	34.1	
Derris-magnesium carbonate	10.20	6	233	46	19.7	24.8
Timbo-magnesium carbonate	10.10	6	262	93	35.5	
Barbasco-magnesium carbonate	10.00	6	222	39	17.6	
Derris-tobacco filler	11.85	6	255	16	6.3	27.0
Timbo-tobacco filler	11.83	6	252	99	39.3	
Barbasco-tobacco filler	11.88	6	247	89	36.0	
Derris-hydrated lime	12.50	6	275	18	6.5	25.2
Timbo-hydrated lime	12.52	6	287	118	41.1	
Barbasco-hydrated lime	12.55	6	269	73	27.1	
Derris-hydrated lime [3]	12.50	8	321	302	94.1	93.2
Timbo-hydrated lime [3]	12.52	8	343	324	94.4	
Barbasco-hydrated lime [3]	12.55	8	339	309	91.1	
Check	-------	17	644	22	3.4	3.4

[1] 9 parts of diluent to 1 part of rotenone-bearing roots.
[2] The buffer was made from M/20 solution of potassium acid phthalate and M/15 solution of potassium acid phosphate which were adjusted to pH 4.5.
[3] Unmoistened sample.

From the results of the relative toxicity tests of kerosene extracts of the various dust samples shown in table 3, it is apparent that the alkaline dust mixtures talc, magnesium carbonate, tobacco filler, and hydrated line when moistened cause significant losses in toxicity of rotenone-bearing plants. The fact that timbo retains much of its toxicity to houseflies in the higher alkaline ranges may be explained by the presence of a larger percentage of resinous materials in the plant sample. This would indicate that rotenone is the major ingredient that is deteriorated by the alkalinity of the dust mixtures. Marked deterioration was evident in all samples more alkaline than pH 7.16.

In preliminary tests with identical dust samples used on cabbage-worms, the addition of sulfur had improved the toxicity of the rotenone-bearing dusts. Consequently, sulfur was added to the highly alkaline diluents at the rate of 1 pound of the diluent to 9 pounds of sulfur. This mixture was maintained at approximately 48 percent moisture and stored as previously described. Although these dust samples remained alkaline after the addition of sulfur, they showed practically no loss in toxicity when tested on houseflies (table 4). Oil filtrates of a dust containing only sulfur and the diluent exhibited almost no toxicity to houseflies.

The entries in tables 3 and 4 that show the percentage of flies killed (columns 6 and 7, respectively) are the weighted means of the replications in each test. By the substitution of letters for degrees of significance, as in tables 5 and 6, a comparison can be made of any insecticidal dust with another in the same row of the table. Where the letters are identical, the two observed "percent killed" were not

sufficiently different to be judged significant at the 5-percent level of significance. However, if different letters are associated with them, it is implied that the difference is significant. This interpretation of letters applies only when reading across a row, and these letters cannot be used for comparisons within a column of the table. Where two letters occur together, the observed percent kill of this dust lay between the values found for the dusts having these letters as indices and was not significantly different from either. The dusts corresponding to the italic letters did not give consistent percent kills in their subsamples, so that the letter by which they are designated/may be in error in one direction of the other. In the case of the entries corresponding to talc in table 5, however, there can be no doubt that the talc dusts give significantly lower percent kills than those to the left of them in the table, since there is a strong line of demarcation at this point in the pH scale, as can be seen in table 3.

TABLE 4.—*Percentage kill of houseflies by kerosene extracts of Derris, Timbo, and Barbasco dust mixtures containing sulfur, when tested after a 7-day period in damp storage*

Rotenone-bearing dust [1]		pH	Tests made	Flies tested	Flies killed		Average kill
Root	Diluent [2]						
			Number	*Number*	*Number*	*Percent*	*Percent*
Derris	Magnesium carbonate	9.00	6	252	237	94.0	
Timbo	do	9.07	6	238	229	96.2	96.1
Barbasco	do	9.17	6	241	237	98.3	
Derris	Tobacco filler	9.03	6	277	276	99.6	
Timbo	do	9.33	6	270	268	99.2	99.2
Barbasco	do	9.50	6	273	270	98.9	
Derris	Hydrated lime	11.23	6	275	269	97.8	
Timbo	do	11.46	6	264	241	91.2	95.3
Barbasco	do	11.17	6	276	268	97.1	
	Sulfur		8	334	12	3.5	3.5
	Check		11	354	11	3.1	3.1

[1] 9 parts of diluent to 1 part of rotenone-bearing roots.
[2] Contained sulfur at rate of 9 parts to 1 of diluent by weight.

The letter "g" has been used here in connection with the check to emphasize the great difference between the check and the other entries in the table and the similarity of the behavior of the check in all the experiments.

TABLE 5.—*Statistical significance of data in table 3* [1]

Rotenone-bearing root	Significance for diluent indicated [2]									
	Sulfur	Gypsum	Buffer	Calcium sulfate	Talc	Magnesium carbonate	Tobacco filler	Hydrated lime	Unmoistened hydrated lime	Check
Derris	a	a	b	d	*e*	e	f	fg	c	g
Timbo	a	a	*b*	b	c	d	cd	c	b	g
Barbasco	a	b	a	c	*d*	f	d	e	c	g

[1] Computed from original replications from which the data in table 3 were obtained by using the χ^2 table for 1 degree of freedom and the 5-percent level of significance:

$$\chi^2 = \frac{[P_1 - P_2]^2}{P[1-P]\left\{1/N_1 + 1/N_2\right\}}, \text{ with } P = \frac{N_1P_1 + N_2P_2}{N_1 + N_2}.$$

[2] See text for significance of letters.

TABLE 6.—*Statistical significance of data in table 4* [1]

Rotenone-bearing root	Significance for diluent indicated [2]			Sulfur	Check
	Magnesium carbonate	Tobacco filler	Hydrated lime		
Derris	*b*	a	a	g	g
Timbo	*b*	a	c	g	g
Barbasco	*a*	a	a	g	g

[1] See footnote 1, table 5.
[2] See text for significance of letters.

SUMMARY

Diluents used in the preparation of rotenone-bearing dusts show a wide range in hydrogen-ion potential which is of considerable importance in the utilization of such materials as plant insecticides.

Rotenone-bearing dusts prepared from highly alkaline diluents and kept in damp storage in the absence of light for a period of 7 days, exhibited little or no change in pH, but showed considerable loss in toxicity when used in kerosene extracts in tests with houseflies.

Parallel acid dust samples kept under identical storage conditions retained their toxicity to the housefly. Dry or unmoistened alkaline and acid samples remained unchanged in this respect.

The addition of sulfur to the alkaline dust mixtures prevented deterioration of the rotenone-bearing dust mixtures under the conditions of this experiment.

THE REPRODUCTIVE EFFICIENCY OF THE ALBINO RAT UNDER DIFFERENT BREEDING CONDITIONS[1]

By M. J. BABCOCK, *assistant in animal nutrition*, R. BOGART, *assistant in animal physiology*, G. SPERLING, *research instructor in animal nutrition*, and S. A. ASDELL, *professor of animal physiology, department of animal husbandry, New York (Cornell) Agricultural Experiment Station.*

INTRODUCTION AND REVIEW OF LITERATURE

The problem of determining the most efficient breeding age for animals is an old one, but quantitative data on the subject have been obtained only comparatively recently. In 1909 Mumford started a thorough study at the Missouri Experiment Station on the growth and reproduction of swine under various regimes, which has been continued to the present time. McKenzie (*11*) [2] summarized the results previously reported in detail by the other Missouri workers. Table 1 presents averages from their data. The litters from the sows which were bred early and those which were bred at a normal age were approximately equal in weight and in number of young. The group of sows that were bred late, on the other hand, had much smaller litters. The sows that were bred early (while they were still in the growing period) were considerably retarded in growth by the added demands of raising their first litters, but they continued to grow twice as long as did the others. They therefore reached about the same ultimate size as the sows of the other groups. Carmichael and Rice (*3*) carried out a somewhat different experiment, also with swine, and in general confirmed the Missouri results as far as the growth trends were concerned.

TABLE 1.—*The effect of age at which sows were bred upon the weight, number, and and vitality of their young*[1]

Period of sow's life when bred	Age of sows	Birth weight of young	Total litter weights at birth	Young per litter at birth	Young alive after 12 hours	Young weaned	Mature weight of sows
	Days	*Pounds*	*Pounds*	*Number*	*Number*	*Number*	*Pounds*
Early in life	218.1	2.30	20.01	8.68	6.62	4.42	415.3
At normal age	478.6	2.38	19.86	8.36	7.72	6.36	401.0
Late in life	837.6	2.85	14.91	5.62	5.06	4.00	384.4

[1] Data from Missouri Agricultural Experiment Station Research Bulletin 118, tables 1 and 3 (for mature weight of sows).

With dairy cattle, early breeding has the special advantage of bringing the heifer into milk production sooner, in addition to the value of the calf produced. The Missouri workers, Eckles and Sweet (*6*), demonstrated, however, that lactation markedly retards growth, as measured by weight and skeletal size. They found that if lactation occurs early the mature size of the animal will be affected.

[1] Received for publication December 11, 1939. These studies were supported in part by a grant from Bankhead-Jones project 14, and in part by a grant from the Rockefeller Grant for Research in Longevity.
[2] Italic numbers in parentheses refer to Literature Cited, p. 852.

For sheep, Briggs (*2*) found that ewes bred at their first season had a slower growth rate than ewes bred later, but that they reached the same ultimate size. They also produced rather more than half a lamb extra, but more dental defects became apparent as they grew older.

The work of Bogart et al. (*1*) with rats has shown quite definitely that pregnancy exerts a strong stimulus on growth while lactation as definitely retards growth. Slonaker (*14*) and Cole and Hart (*4*) have obtained similar results using somewhat different methods. It may be noted here that none of the work quoted has shown the existence of the pregnancy stimulus in the domestic animals. This may possibly be owing to the fact that other conditions in these experiments were not kept as uniform as they have been in the rat experiments. Another possibility is that the pregnancy stimulus can only make itself felt when the potentiality for growth is still fairly great. The rat seems to be peculiar in that it retains growth potentialities until quite late in life (*10*). The writers have obtained the pregnancy growth stimulus even in rats bred at 280 days (the normal breeding age is about 100 days, and puberty about 65 days).

Other factors of importance in the over-all efficiency of breeding animals are the number of young produced at a time and the interval between their production. This has rarely been investigated in domestic animals as it means that the animals have to be kept for their whole lilfetime whether they are economically efficient or not. Most of the reports which have been made on the subject have grouped animals, such as early, normal, or late breeders, according to their behavior. This method of grouping does not tell which is the best regime to follow since an individual falls into its class because it is unable to do otherwise. It tells what happens as a rule, but not what should be encouraged to happen in order that the best results may be obtained.

The writers made a study of the effects of various reproductive regimes on albino rats to determine which one should be followed in order to get the optimum breeding results. Rats were used because they have a much shorter and more prolific life than the domestic animals. The data in the present paper are a part of the information collected in the study.

EXPERIMENTAL PROCEDURE

Four groups of 50 female albino rats each were used to test the differences in the over-all reproductive efficiency of the various breeding regimes. The rats were all born about the same time. The division into groups was made at random, except that litter mates were put into different groups. The groups were bred as follows:

Group 1 was bred as early as the rats would breed and is referred to as the bred-early group.

Group 2 was bred at the normal breeding age (100 days), and is referred to as the bred-normal group.

Group 3 consisted of rats whose breeding was deferred until the animals were 280 days old. This group is referred to as bred late.

Group 4, like group 2, was bred at the normal breeding age, but the rats were not allowed to suckle their young and were bred as soon as possible after parturition. This group is referred to as young killed.

The rats were kept in cages containing five females each. They had constant access to the usual stock diet for the station rat colony and water. Also each cage always contained one male. These males were

shifted every week from one cage to the next within the same group. Whenever a male was found to be defective in any way he was immediately replaced. All males were replaced by young males when they were a year old.

When the females became pregnant, as detected by palpation, they were isolated, and with the exception of group 4 were allowed to rear their young to 3 weeks of age. At this time the young were weaned and the females returned to their respective breeding cages. If the young did not survive until weaning time, the females were nevertheless kept isolated for 3 weeks following the date of parturition. The females of group 4, however, were returned to their breeding cages within 1 day after parturition. Complete records were made of the number, weight, and sex of all young at birth and at weaning.

The data recorded here refer only to litters born on or before the rats were 671 days old, since subsequent data were rendered useless by the accidental killing of 60 animals. Abortions, when they were seen, were charged against the rat as the production of a zero litter since they represent an attempt at reproduction and the loss of so much time and efficiency. When all the young were dead at birth, this also was charged against the rat as a zero litter for the same reason. Other young born dead were not counted in this work as they do not represent productive reproduction. Females which were sterile from the outset of the experiment were included in the groups; there was no way of determining whether the sterility was caused by the reproductive regime.

Examination of tables 2 and 3 shows that the reproductive efficiency of group 1, as measured by the number of litters and the number and weight of living young at birth and at weaning, was somewhat less than that of the animals bred at a normal age. The difference amounts to 9.1 percent for the number born in favor of group 2. This is in spite of the earlier start by the rats that were bred early. Group 1 has a slightly better weaning percentage, but the number weaned is still 8.8 percent greater for group 2. From the data there appears to be no advantage in early breeding, but slightly the reverse.

TABLE 2.—*The effect of age at which female rats were bred, and of killing their offspring at birth, upon the weight, number, and vitality of their young*

Group No. [1]	Litters	Young alive at birth	Weight of young alive at birth	Young alive at weaning	Weight of young alive at weaning	Average maximum weights of nonpregnant females
	Numbers	*Number*	*Grams*	*Number*	*Grams*	*Grams*
1, bred early	426	2,487	14,374	1,974	62,773	310.3
2, bred at normal age	436	2,714	15,731	2,148	68,618	308.6
3, bred late	255	1,257	7,447	898	30,224	296.3
4, young killed	660	3,984	22,743	----------	----------	323.9

[1] See text for explanation of groups; there were 50 rats in each group.

The females of group 3 had by far the smallest number of litters and the smallest sized litters. In accordance with the usual finding that the weight of the young varies inversely with the number in the litter, individual young of this group averaged slightly heavier than those of other groups. However, it should be noted that the young of group 1

were not larger than those of group 2 although their litters were appreciably smaller than the litters of the latter.

TABLE 3.—*The effect of age at which female rats were bred, and of the killing of their offspring, upon the weight, number, and vitality of their young, the results being expressed on a per-rat basis* [1]

Group No.[2]	Litters per rat	Young per litter at birth	Young per rat	Weight of young at birth	Weight of young at weaning	Young weaned
	Number	*Number*	*Number*	*Grams*	*Grams*	*Percent*
1, bred early	8.5±0.35	5.80±0.07	49.7±2.11	5.78	31.8±0.09	79.4
2, bred at normal age	8.7±0.29	6.22±0.08	54.3±1.86	5.80	31.9±0.10	79.1
3, bred late	5.1±0.23	4.90±0.11	25.1±1.29	5.92	33.7±0.15	71.4
4, young killed	13.2±0.50	6.04±0.07	79.7±3.02	5.71	----------	----------

[1] Probable errors shown.
[2] See text for explanation of groups; there were 50 rats in each group.

Statistical analysis shows that in the numbers of litters per rat the difference between group 1 and 2 is not significant. Groups 3 and 4, however, are significantly different. In the number of young per litter at birth the animals of group 1 are significantly lower than those in group 2, but those in group 4 are not. The rats in group 3 are significantly lower. In the number of young per rat, group 1 is not significantly lower than group 2. The difference is twice the probable error. Groups 3 and 4 differ significantly from group 2. No analysis is possible of the weights at birth as these figures were obtained by dividing the sums of the weights of the whole litters by the total number born. The difference in the weight of young at weaning is not significant between the groups 1 and 2, while the increased weight of young in group 3 is very significant. This is associated with the smaller litters and the high mortality which probably gave the young more milk each and assisted in the culling of many of the unfit. The percentage of young weaned is a percentage of the whole, and not a litter by litter average, so these figures are not analyzed.

Group 4 was able to have a considerably larger number of litters since the rats were rebred immediately after parturition instead of 3 weeks later. Their litters averaged slightly less in number of young, but they produced 47 percent more young than those in group 2. This was despite the fact that two of them produced no litters. This very intense production was not an undue drain on the females, on the contrary they made the best growth of all the groups considered in this paper. This is shown in table 2 which reports the average maximum weights of nonpregnant animals in each group. Lactation is a far greater drain on the mother than reproduction, even of the most intense kind. Indeed, pregnancy must be regarded as a stimulus, or more probably as the means of removal of an inhibitor for growth. This inhibitor is believed to be estradiol, since virgin rats attain a much lower ultimate weight than bred rats, while ovariectomized rats attain the largest size.

It may be noted in passing that group 4 had considerably larger litters than group 2 early in life, but that the litter size dropped off markedly so that in later life their litter size was less than that of group 2.

In order to compare the reproductive efficiencies of the different groups in more detail, the reproductive patterns are given in table 4.

TABLE 4.—*The effect of age at which female rats were bred, and of killing their offspring at birth, upon their reproductive patterns*

Group No.[1]	Sterile rats	Rats having only 1 litter	Rats not reproducing after 1 year of age	Litters conceived within 8 days after rats were rebred
	Number	*Number*	*Number*	*Percent*
1. Bred early	0	4	13	65.8
2. Bred at normal age	0	2	7	69.6
3. Bred late	2	2	6	62.2
4. Young killed	2	0	8	72.1

[1] See text for explanation of groups; there were 50 rats in each group.

A study of table 4 shows that the lower reproductive efficiency of the group 1 in comparison with group 2 involves three factors: (1) A larger number of the rats in group 1 had ceased to reproduce by the time they were 1 year old; (2) a smaller percentage of the litters were conceived within 8 days after parturition, that is, a larger percentage of the litters were irregular in conception, thus spacing the litters further apart; and (3) the litters were smaller (table 3).

These factors more than compensate for the earlier start of the rats in group 1. Group 3 had a decidedly lower over-all reproductive efficiency because (1) it had a great handicap in not starting breeding as soon as the others, (2) it had the most delays, that is, the most irregular litters, and (3) it had considerably smaller litters (table 3).

Group 4 owes its efficiency to the fact that these rats did not lose the 3 weeks required to rear their young. Also, the females were in better condition and therefore had more litters which were more regularly conceived.

The group 3 rats had more difficulty in rearing their young than did the other groups so that the percentage weaned is considerably lower than in the other groups. This is in spite of the fact that they had smaller litters to rear, a fact which is reflected in the greater average weaning weights in this group, though the average increase in weight at weaning does not outweigh the greater loss of young. Group 3 lost 70 litters entirely during lactation as compared with 46 litters for group 1, and 57 for group 2. If these figures are taken at their face value it would indicate that early breeding is decidedly favorable for the establishment of good lactation. Table 3 does not reveal, however, a higher level of lactation for the individual rats of group 1.

DISCUSSION

In general the data are in agreement with the results of other workers. The results indicate perhaps that early breeding has some deleterious effects but that these are not great. They do not suggest that early breeding should be resorted to as a breeding practice, but naturally in work of this sort it is necessary to determine the effects from one species to another. The lifetime efficiency in groups studied as a whole is essential for such work, and culling immediately destroys its value. If the animals are not in the best of condition and if the breeding occurs very early, the practice will usually result in somewhat inferior young and slightly stunted females. This would suggest a compromise in practice, where conditions are usually not optimum. Breeding late is definitely uneconomical.

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The data on the rats in group 4 show a relatively smaller litter size as compared with those classed as normal than that found by Slonaker (*14*, *16*). But his numbers were meager, and the conditions of the experiment were not quite the same as those in the present experiment. The growth of the females used in the present study is in partial disagreement with the data of Cole and Hart (*4*), but their animals were subjected to other conditions which may have affected the results. Slonaker's rats were divided between stationary and rotary cages which altered the reproductive regime somewhat, and the rats of Cole and Hart were injected with mare gonadotropic hormone.

The rats used by the present writers did not show any significant variation in the number of mammary tumors which occurred before they were 22 months of age. Two of the females in group 4 and one in each of the other groups had these tumors.

The data show that rats which were not subjected to lactation were able to carry through a much larger number of gestations. It has been repeatedly shown that lactation is a much more severe tax on the animal than is gestation. The increased demands made by lactation are reflected by the increased food consumption (*5*, *12*, *13*, *15*); by the negative mineral balance (*7*, *8*), and by the change in composition of the body tissues (*9*).

SUMMARY

The reproductive efficiency of the albino rat under various reproductive regimes was investigated. Four groups of 50 rats each were studied until they were 22 months of age. A total of 1,777 litters were studied. The over-all reproductive efficiency of group 1 (early bred) as measured by the total number and weight of young produced was somewhat less than that of the rats bred at a normal age, and the reproductive efficiency of the group in which breeding was delayed until 9 months of age was very much lower than that of any of the other groups. They also experienced much more difficulty in lactation.

The animals which were not allowed to suckle their young and which were rebred immediately after parturition, produced many more young than did the groups which were subjected to lactation.

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U. S. GOVERNMENT PRINTING OFFICE: 1939

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